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The Occurrence of *Hadromys* (Rodentia: Muridae) in Early Pleistocene Siwalik Strata in Northern Pakistan and Its Bearing on Biogeographic Affinities Between Indian and Northeastern African Murine Faunas

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ABSTRACT

Three upper molars collected from an early Pleistocene site in the Soan Formation of the Upper Siwaliks outcropping in the Pabbi Hills of northern Pakistan are described as a new species of *Hadromys*. That genus was known only by the living *H. humei*, which is found in northeastern India. Compositions of the murine faunas of northeastern India, northern Pakistan, and Pleistocene Pakistan are compared. Because the new *Hadromys* is associated with fossil species of *Golunda*, another Indian native, and because that

genus has also been identified in Pliocene sediments of Ethiopia, morphologies of specimens in samples of Recent and fossil *Golunda* are contrasted. *Golunda* remains an Indian region endemic; the Ethiopian species is not a member of that genus and is known only from northeastern Africa. Biogeographical relationships between the Indian subcontinent and northeastern Africa as indicated by Recent and fossil murine faunas are discussed.

INTRODUCTION

With the publication in 1978 of a report on fossil Muridae from Neogene Siwalik de-

posits in northern Pakistan, Dr. Louis L. Jacobs opened a window on past species di-

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versity of murine rodents in central Asia. The view he provided has significantly influenced the ways other glirologists are looking at possible evolutionary histories that resulted in the modern murine fauna now composed of more than 450 species (Carleton and Musser, 1984). The Siwalik sediments containing murine fossils were deposited between 14 and 1.6 million years ago (Barry et al., 1985; Jacobs et al., in press; Lowrie and Alvarez, 1981) and yielded samples of isolated molars and incisors representing 8 genera and at least 11 species. The deposits contain *Antemus chinjiensis*, the oldest known murine, which according to Jacobs (1978) possessed a morphology from which all other murines could be derived. Miocene species of *Progonomys*, *Parapodemus*, and *Mus* comprised one primary branch that Jacobs derived from basal *Antemus*-like stock; Miocene species of *Karnimata* and *Parapelomys* formed another branch emerging from the *Antemus* trunk. Pleistocene samples of *Golunda* and another form that Jacobs tentatively assigned to *Rattus* represented twigs originating from the *Karnimata-Parapelomys* stock. Living species of *Apodemus*, *Mus*, *Acomys*, *Praomys*, and their allies form the crown of the *Progonomys* branch; from the *Karnimata* branch has leafed the contemporary species of *Rattus*, *Arvicanthis*, *Pelomys*, *Mylomys*, *Golunda*, and their relatives. From Miocene beginnings, as interpreted by Jacobs, the evolutionary diversity of murines flourished over Asia, Africa, and Europe.

Results of Jacobs' study have been used as a frame of reference by others studying Neogene assemblages of fossil murines. Subsequent to publication of his descriptions and comparisons, additional murine fossils from northern Pakistan have been described and their significance discussed by Cheema et al. (1983) and Wessels et al. (1982). The diversity of fossil rats and mice in central Asia suggested by the Pakistan samples has been increased by discovery of new species from Miocene and Pliocene sediments in Afghanistan (Brandy, 1979; Brandy et al., 1980; Sen et al., 1979; Sen, 1983); the interplay of past faunas between Asia and Africa has been touched on not only by Jacobs (1978) but also by those reporting on compositions of Pliocene murine faunas from northeastern Africa

(Sabatier, 1982; Wesselman, 1984, for example).

As a student of living murines, particularly those native to Asia and the Indo-Australian region, I turn often to morphologies and temporal distributions of fossil murines, seeking insights into origins of patterns of phylogenetic relationships and geographic distributions reflected among contemporary murine species. Asian fossils, particularly those from the Pliocene to Recent time period, are especially important to the understanding of links between ancient and modern faunas. However, the uncritical use of the genus *Rattus* as a catchall for many species of fossil murines presents a major hinderance. My research has demonstrated that many contemporary species conventionally assigned to *Rattus* (Ellerman, 1941, for example) are only distantly related to *Rattus* proper, and I have accordingly reclassified them (Musser, 1981, 1982; Musser and Newcomb, 1983, for example). Similarly, I have encountered difficulties with certain samples of Pleistocene taxa; for example, fossils from Pleistocene Chinese outcrops originally identified as *Rattus* (or its synonym *Epimys*) but which proved to be examples of *Niviventer* and *Leopoldamys* (Musser, 1981).

Jacobs' (1978) identification of three isolated molars from early Pleistocene Siwalik sediments as cf. *Rattus* sp. suggested the possibility of another species erroneously referred to that genus. Dr. Jacobs was very generous and did not hesitate to send me the three teeth. I studied them, took measurements, subjected them to strong microscope lamps and electron blasts from the scanning electron microscope, managed not to drop any, and did not lose a single tooth. My identification of those small, isolated upper molars as well as their significance in understanding the present and past distributions of Asian murines form the substance of this report.

The fossils are a sample of an extinct species of *Hadromys*.² Its closest relative is the living *H. humei*, a native of northeastern India. To

² Another view has recently been provided by Gaur (1986: 543), who in reporting on a new fossil murine from the Upper Siwaliks of India states that "cf. *Rattus* of Jacobs is more related to *Nesokia*, with which it shares

place description and comparisons of the fossils in proper context, I begin the report with a redescription of *H. humei* that is meant not as a definitive account but as an introduction to this poorly known member of the Indian fauna. My knowledge of the species comes from study of skins, skulls, and dentitions along with the scanty ecological and distributional data available in published accounts. This information sets the stage for the next section describing the fossil species of *Hadromys* and comparing it with *H. humei*. The part that follows discusses relationships between the two species of *Hadromys*, between *Hadromys* and *Rattus*, and between *Hadromys* and genera in the arvicanthine group, particularly *Golunda*. Faunal and habitat associations are then provided which contrast the Pleistocene and modern murine assemblages of northern Pakistan with the modern fauna native to northeastern India.

A next-to-last section discusses biogeographic relationships of the faunas in northern Pakistan and northeastern India at the level of species and then genera. I focus on *Golunda*, which is a constituent of both living and early Pleistocene murine associations in northern Pakistan, has been identified from Pliocene sediments in northeastern Africa, and is currently considered to be a close relative of the living African *Mylomys*. I compare samples of Asian *Golunda* with African *Mylomys* and then with the African Pliocene samples of *Golunda*. My interpretations of phylogenetic and biogeographic relationships derived from morphologies in those samples contrast with current views. Finally, I discuss generic limits in *Hadromys* and intercontinental affinities between Asian and African murines.

ABBREVIATIONS

DP	Dartmouth College-Peshawar University Pakistan Project
AMNH	American Museum of Natural History, New York

BM	British Museum (Nat. Hist.), London
FMNH	Field Museum of Natural History, Chicago

METHODS

Specimens I examined are in collections of the institutions listed above. Casts of fossils are in the American Museum of Natural History. Specimens requiring identification are noted in text, legends to figures, and tables. Values I obtained from measuring certain specimens are listed in either table 2 or legends to figures; limits of the measurements are explained in the legend to table 2.

Much of the report focuses on comparisons of dental traits among taxa of fossil and modern species. The nomenclature I use for cusps (also called cones or tubercles by other authors) and cusplets (sometimes referred to as cuspids or cuspules) is diagrammed in figure 1. The terminology brings together those proposed by Miller (1912) and van de Weerd (1976) and is a combination I have used in my previous publications on muroid rodents. Other systems of names and notations have been proposed (see table 3 in Jacobs, 1978), including a descriptive terminology suggested by Jacobs (1978) in his report on Siwalik rodents. The nomenclature he applies to most parts of molars reflects homologies with dental structures in other groups of muroid rodents and even mammals that are not rodents. For that reason his arrangement is better than most of the others but I still have problems with homologies of certain structures in his scheme and until I find solutions I will stick to the terms shown in figure 1.

Another item of terminology needs explanation. When Jacobs (1978) wrote of Neogene Siwalik Muridae, he was referring to a group of more than 450 species of rats and mice that are native to the Old World. His usage excluded hamsters (Cricetidae), voles (Arvicolidae), gerbils (Gerbillidae), and other groups of muroid rodents from the Muridae. Throughout this report I refer to Jacobs' Muridae as murines, which reflects the arrangement of Carleton and Musser (1984) in which the Murinae and 14 other Recent groups of muroid rodents are listed as subfamilies of Muridae.

many morphological characters and differs only in the absence of posterostyle, than to any *Rattus* species (J. J. Jaeger, personal commun.)."

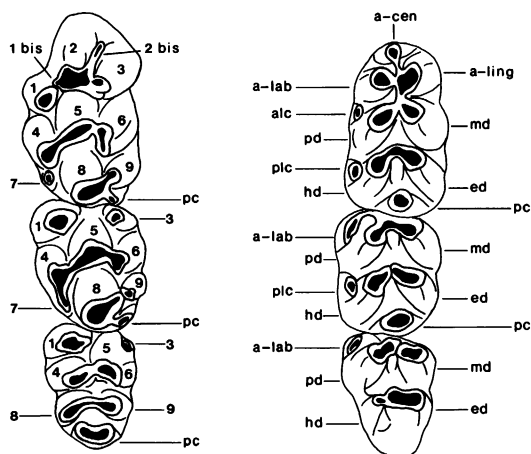


Fig. 1. Nomenclature of dental structures: a diagram of upper and lower molar rows in *Leno-thrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in text with the prefix *t*; *pc*, posterior cingulum. Lower molars: nomenclature is slightly modified from that used by van de Weerd (1976); *a-cen*, anterocentral cusp; *a-lab*, anterolabial cusp; *a-ling*, anterolingual cusp; *pd*, protoconid; *hd*, hypoconid; *md*, metaconid; *ed*, entoconid; *pc*, posterior cingulum; *alc*, anterior labial cusplet; *plc*, posterior labial cusplet.

ACKNOWLEDGMENTS

John Hill and Paula Jenkins allowed me to use the collection at the British Museum (Nat. Hist.) and helped me when I encountered problems. Loan of specimens from the Field Museum of Natural History were approved by Bruce Patterson. Louis Jacobs sent fossils and arranged for casts of all the Siwalik murines to be delivered to me. I thank all for their kindness and interest in helping me realize results of my research.

Scanning electron micrographs were made by Lauren Duffy, Joan Whelan, and Andrew Simon. Peter Goldberg is responsible for the photographic prints. I am grateful to them for their care in producing results of high quality.

Contributions to the report were made by Louis Jacobs, Lawrence Flynn, and Michael Carleton who took time from their busy research and teaching schedules to read the manuscript and give me the benefit of their critical reviews.

THE LIVING SPECIES OF *HADROMYS*

Among a large collection of birds and mammals given to the British Museum (Nat. Hist.) by Allan O. Hume in the late 1800s were six small rats from Moirang, Manipur State, which Oldfield Thomas studied and named *Mus humei*. In his diagnosis, Thomas (1886a: 84) wrote that *humei* was "Externally similar in almost every respect to *Golunda Elliotti*, Gray but with the ungrooved incisors and narrow molars of true *Mus*. Front edge of anterior zygoma-root concave, as in *Mastacomys fuscus*, Thos., and some other Australian Muridae." An expanded description of *M. humei* was published later that same year (Thomas, 1886b).

Toward the close of the 19th century, the genus *Mus* embraced most species of rats and mice that had been described and named up to that time. By 1911 biologists realized that the genus should be restricted to a cluster of species with certain shared morphological traits and that the vast range of variation in morphologies and geographic distributions characterizing all the other samples represented monophyletic groups that should be excluded from *Mus*. The Manipur rat constituted one such group and Thomas (1911: 999) recognized its distinctive traits by placing it in the genus *Hadromys*. His diagnosis and description of the new genus was short:

General appearance as in *Golunda*. Form stout. Tail rather short. Sole pads six. Fifth fore toe very short; fifth hind toe reaching just to base of fourth. Mammæ 2-2 = 8. Skull shaped almost exactly as in *Golunda*, with the same short muzzle and well marked supra-orbital and parietal ridges. The anterior edge of the zygomatic plate is however concave, and the posterior palate ends behind the last molar. Incisors very broad and heavy. Molars wholly unlike those of *Golunda*, more like those of *Epimys*, rather hypsodont, with laminae well defined. No unworn specimens are however available for examination.

Mus humei Thomas (1886a) was designated the genotype of *Hadromys* and constituted its only known species.

For many years the only specimens of *Hadromys* were the six from Moirang described

by Thomas (1886a, 1886b). By 1926 another rat had been collected, this time from Anarakhata at 300 ft elevation in Kamrup District, Assam State (Hinton and Lindsay, 1926). Finally, during the late 1940s and early 1950s, larger samples were obtained from Imphal and Bishampur in Manipur State at elevations between 3500 and 4000 ft (Roonwal, 1949, 1954; Ellerman, 1946, 1961), and from Karong, Manipur (FMNH 76562 and 76567). Thought to be rare for so many years, *H. humei* has turned out to be common when special efforts were made to collect it.

Although *H. humei* is not rare at some localities, it is uncertain if samples in museum collections accurately reflect its geographic distribution. Available data locate the species within a small area in northeastern India only. Coupled with scanty knowledge of distributional limits is the meager information on habitat and habits. The only ecological observations are those of Roonwal (1949: 106), who reported that nearly all *H. humei* in the Imphal region of Manipur were taken in oak parkland. This habitat consists of scrublike scattered oak trees (30–40 ft high) on dry hillsides. Tall grass (10–12 ft high) covers the ground between trees, shrubs are scarce, and epiphytes absent. The soil is loamy, rocky, and has little humus. Except for the high grass, the countryside appears parklike, partly due to undulating hills and partly to the tall and thinly spread trees (Roonwal provides a photograph of that habitat in plate IV). His further note that the “stomach of an adult male trapped in oak scrub contained mainly finely cut grass leaves” is the only solid data about habits but does reflect cranial and dental morphology as I will explain below.

Thomas' (1886a, 1886b) original description of *Hadromys humei* combined with additional notes made by subsequent observers (Roonwal, 1954; Ellerman, 1961) describe a terrestrial rat of small body size with a tail longer than combined lengths of head and body, long hind feet, and soft dense fur (table 1; fig. 2). Upperparts of most of the head and body are dark grayish brown sprinkled with black and either white or yellow, an effect created by some hairs that are all black and others that are pale yellow or unpigmented. Toward the back there is a transition to red-

TABLE 1
Measurements (in Millimeters) of Adult
Hadromys humei^a

Measurement	$\bar{x} \pm SD$	OR	N
Length of head and body	107.8 \pm 6.0	98–120	22
Length of tail	124.6 \pm 5.9	112–138	22
Length of hind foot	25.1 \pm 1.1	23–28	22
Length of ear	17.7 \pm 1.4	16–22	22
Greatest length of skull	30.3 \pm 1.0	28.4–31.7	18

^a Statistics were computed from values listed by Ellerman (1961: 716 and 717) and obtained from animals caught in Bishampur, Manipur State, India. Lengths of body, tail, hind foot, and ear were recorded by Ellerman from specimen labels; skull lengths are his measurements. The summary listed here is meant to convey nothing more than a general impression of overall body and skull size.

dish hues, the rump, base of the tail, and thighs being tinged with rusty red. Underparts are grayish white tinged with either pale or rich buff. The large and rounded ears, including the inner surfaces of the pinnae, are buffy gray and hairy. Each pinna is set off by a small buffy or orange preauricular patch.

The tail is also hairy but not to the degree that tail scales are hidden. The dorsal surface is brownish black, the ventral surface ranges from pale buff to white; this striking bicoloration characterizes all animals I have seen.

Both front and hind feet are long and slender. Their densely haired dorsal surfaces are grizzled buff. Palms are pale grayish pink, plantar surfaces are darker. Three interdigital pads and two metatarsal pads situated well back of the interdigitals adorn the palm. The first digit, as in most muroid rodents, is rudimentary and supports a nail. The three middle digits are long, and the fifth digit is short, its tip barely reaching the base of the fourth digit (see the drawing in Roonwal, 1954). Each outer digit of the long and narrow hind foot is short, the three inner digits are long and because tips of the outer digits barely reach the bases of digits 2 to 4, the foot appears to have only three long toes. The plantar surface is naked with a pair of interdigital pads at the bases of the three longest digits and another pair set far posterior at the



Fig. 2. *Hadromys humei*. Reproduction of color plate 5 in Thomas (1886b). Note the large and rounded ears, conspicuous contrast between upperparts and underparts of head and body, and bicolored tail.

bases of the outer toes; a small thenar and even smaller hypothelar pads form raised surfaces just behind the most posterior pair of interdigital pads (see the drawing in Roonwal, 1954). Except for the rudimentary thumb, all digits bear moderately long claws.

Each female, as Thomas (1886b) noted, has four pairs of mammae: one pectoral, one postaxillary, and two inguinal pairs.

The cranium of *Hadromys humei* appears compact and robust (fig. 3). From dorsal perspective, the rostrum is short and wide, only slightly broader than the interorbit. Prominent ridges sweep back from the interorbit to the occiput and define a vase-shaped dorsal outline. Sides of the braincase are vertical or nearly so and the interparietal is wide. Zygomatic arches are gently arcuate and the distance from one to the other is only slightly wider than the braincase. Anteriorly each arch broadens into a wide zygomatic plate with a prominent anterior spine that defines a deep zygomatic notch. Sides of the spines nearly touch the rostrum at the nasolacrimal capsules. Those capsules are only slightly swollen

and are plastered against the incisor capsules, which partly define sides of the rostrum.

The deep cranium of *H. humei*, its robust zygomatic arch, and wide zygomatic plate are evident in lateral view (fig. 3). At the back of the cranium the squamosal root of the zygomatic arch springs approximately midway between the bulla and the temporal ridge. The squamosal above the bulla is solid; the squamosomastoid foramen is confined to the suture between squamosal and mastoid. Posterior to the squamosal, the mastoid portion of the petromastoid complex is solid, penetrated only by a tiny mastoid foramen (fig. 4). The auditory bulla is not tightly attached to the squamosal but separated by a moderately large postglenoid vacuity. The alisphenoid strut joins the side of the braincase to the pterygoid ridge and also covers part of the foramen ovale (fig. 4). Posterior to this bony strut is the accessory foramen ovale and anterior to it is the combined masticatory-buccinator foramen. The anterior opening of the alisphenoid canal is clearly evident anterior to the strut. The wide zygomatic plate

has a jutting anterior spine and deeply concave anterior margin. Anterior to the spine is the short and stocky rostrum from which a pair of robust incisors emerge and curve back.

The short rostrum is also apparent in ventral view (fig. 3), as are the wide incisors. The long, narrow, somewhat lyre-shaped incisive foramina are also a prominent ventral feature; the constricted posterior portion ends between the molar rows. Those diverging tooththrows bound a bony palate that is but lightly scored by palatine grooves and ends even with or just beyond posterior margins of the third molars (fig. 4). Posterior to the palate a wide mesopterygoid fossa is breached by spacious sphenopalatine vacuities. At either side of that fossa is a deeply excavated pterygoid fossa that is complete except for the large ventral opening of the foramen ovale in the posterior half. A strong, nearly vertical ridge forms the lateral margin of each pterygoid fossa but this ridge diminishes to a bony thread that continues as a slender bridge over the foramen ovale (fig. 4). The auditory bullae are small relative to size of the braincase and are separated from the pterygoid fossae by moderately large middle lacerate foramina. Their bony eustachian tubes are short and wide and almost touch the small hamular processes. Posteromedial to each bullar capsule is a large stapedia foramen. That opening and the deep groove for the internal maxillary artery beneath the pterygoid bridge, just behind the foramen ovale, conform to a basicranial arterial pattern that is common among species of murid rodents (Musser, 1982; Musser and Newcomb, 1983).

The dentary is short and high (fig. 3). The bony incisor sheath is short and deep, the ventral masseteric ridge is prominent, the coronoid process is small, the angular process large with a moderately wide ventral shelf; there is a concave posterior margin between angular and condyloid processes. The base of the incisor capsule protrudes slightly on the labial side just posterior to the coronoid process.

Upper and lower incisors are wide, deep, and appear strong. The enamel layers are orange and the anterior faces are smooth, without grooves or ridges.

The molars of *Hadromys humei* are broad. Rows of cusps on upper teeth are strongly inclined to the rear, those on lowers slant forward. In each tooththrow, the first molar broadly overlaps the second and the second overlaps the third (fig. 5). A most conspicuous trait, however, is their high crowns (fig. 9), which reflect what Hershkovitz (1962) described as coronal hypsodonty, the vertical elongation of the entire crown of the molar at the expense of the roots. Such hypsodonty is found in molariform teeth that are specialized for crushing and grinding and is typical of grazers. *Hadromys humei*, judged by morphology as well as Roonwal's (1949) single observation of stomach contents, is a grazer, essentially the Manipur murine counterpart of an arvicoline.

A grazing habit is also suggested by occlusal surfaces of upper molars, which are more laminar than cuspidate, especially in adults. The first upper molar consists of two arcuate laminae and a thick, straight posterior lamina (figs. 5, 7). The first and second laminae are each formed of three cusps. The anterolingual cusp (t1) of the first row and the lingual cusp (t4) of the second are columnar and the most well defined of all the cusps in young rats but coalesce with the middle rows of cusps in older animals. The anterolabial cusp (t3) of the first lamina and the labial cusp (t6) of the second are broadly joined to the medial cusps. The posterior lamina is formed of one large, thick central cusp (t8) that is joined to the labial cusp (t6) on the lamina in front by a lateral ridge which is really the small postero-labial cusp (t9) compressed into an anteriorly projecting ridge; that cusp is more distinct in very young adults (I have not seen juveniles) but becomes a connecting ridge between cusps t8 and t6 in older rats (figs. 5, 7).

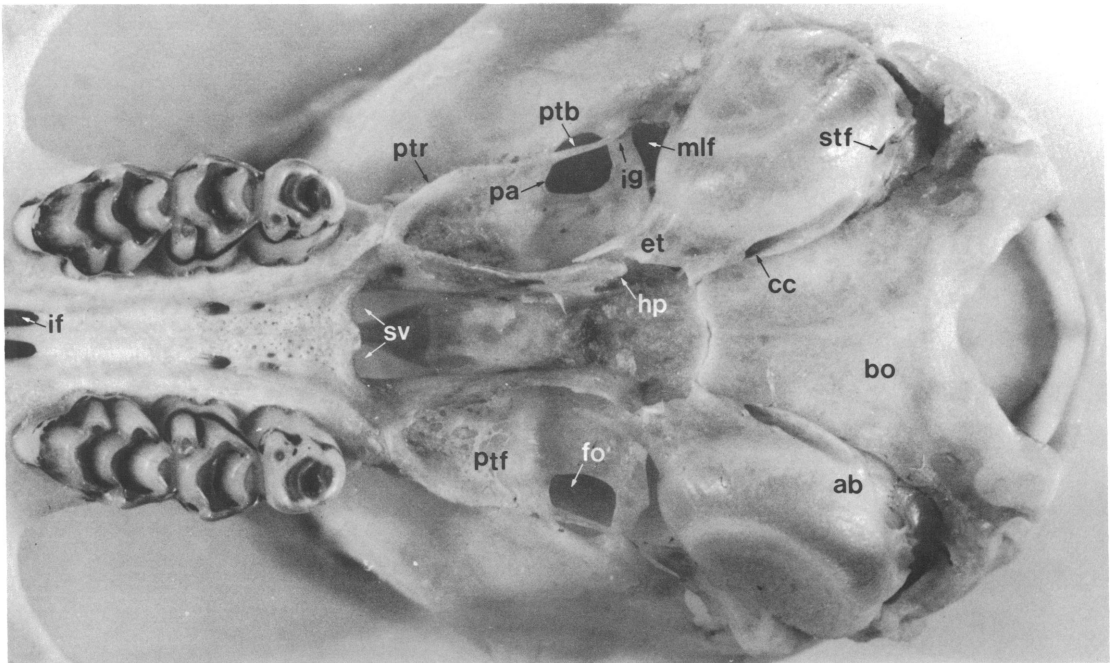
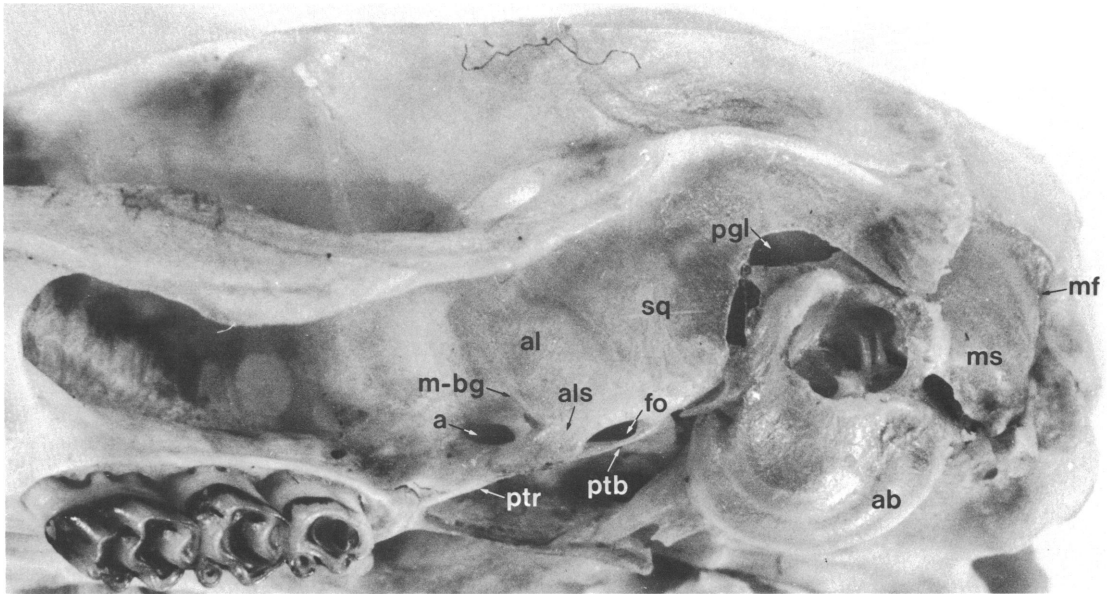
There is a prominent cusp at the anterolingual margin of the second upper molar (cusp t1) but no cusp at the anterolabial corner (cusp t3). The two laminae that form most of the occlusal surface are similar in size and shape to the second and third laminae of the first molar.

The third upper molar is smaller than the others and even simpler in occlusal topography. A large anterolingual cusp (t1), a broad and featureless lamina (formed of cusps t4,



Fig. 3. Cranium and right dentary of an adult *Hadromys humei* (BM 67.110, female) from Imphal, Manipur State, northeastern India. $\times 3$.

Fig. 4. Lateral (top) and ventral (bottom) views of cranium of *Hadromys humei* (BM 67.110). Abbreviations: **a**, anterior opening of alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **als**, lateral strut of alisphenoid bone; **bo**, basioccipital bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale (this is a wide opening partly covered by the bony alisphenoid strut; the anterior portion



of the foramen can be seen just in front of the leading margin of the bony strut; the accessory foramen ovale, which is not labeled, is posterior to the strut and lateral to the foramen ovale); **hp**, hamular process; **if**, incisive foramina where they penetrate between the molar rows; **ig**, groove for the internal maxillary artery; **m-bg**, groove for the masticatory and buccinator nerves, which exit from the anterodorsal margin of the foramen ovale and just medial to the anterodorsal edge of the alisphenoid strut; **mf**, mastoid foramen; **mlf**, middle lacerate foramen; **ms**, mastoid portion of the petromastoid bone; **pa**, posterior opening of the alisphenoid canal (the internal maxillary artery enters the braincase dorsal to the pterygoid platform where the arrow points); **pgl**, postglenoid vacuity; **ptb**, the threadlike pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sq**, squamosal bone; **stf**, stapedial foramen (the stapedial artery enters the bullar capsule through this opening and exits the capsule as the internal maxillary artery); **sv**, sphenopalatine vacuities.

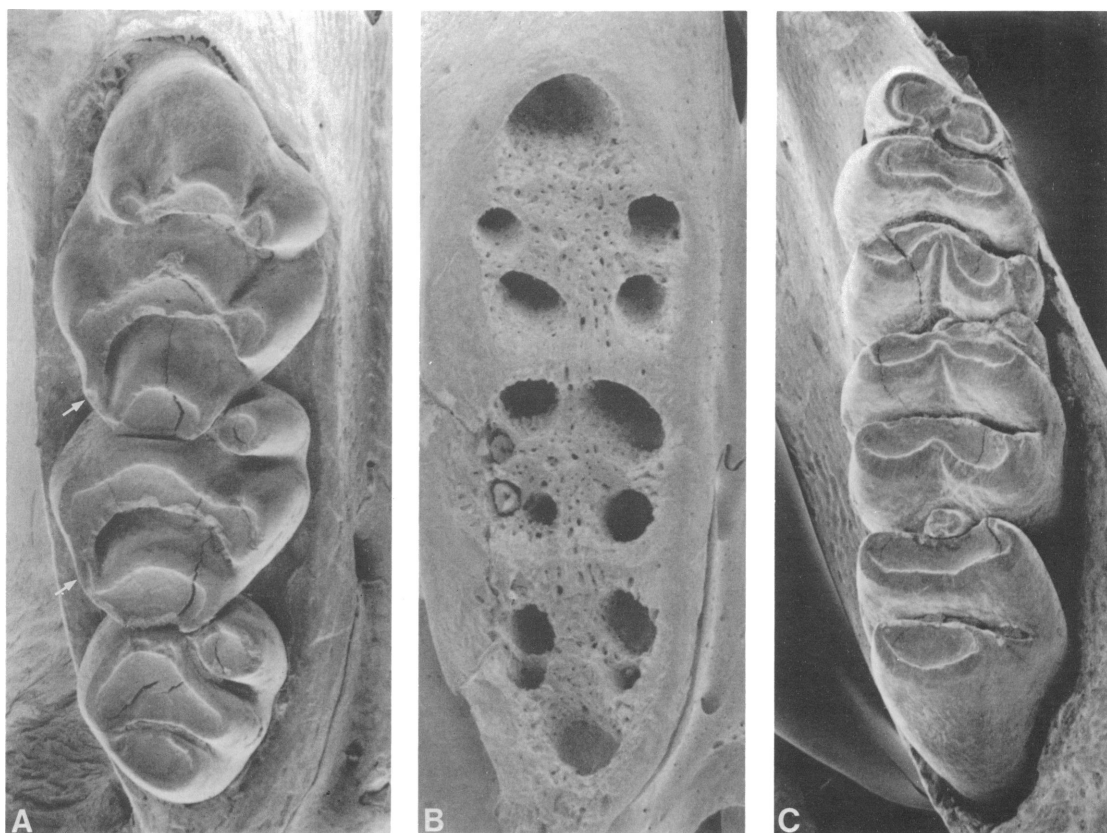


Fig. 5. Right molar rows and root alveoli of young adult *Hadromys humei*. A, upper molars (FMNH 76567; CLM1-3 = 5.5 mm); arrows point to ridgelike cusp t9 on first and second molars. B, alveolar pattern of roots (BM 21.7.8.71; ALM1-3 = 5.7 mm) that anchor upper molars; see text for additional description. C, lower molars (FMNH 76567; CLm1-3 = 5.7 mm).

t5, and t6 so coalesced that their boundaries are not evident), and an oval posterior lamina that seems to consist only of cusp t8 joined at its anterolabial margin to the lamina in front constitute the chewing surface (figs. 5, 7).

The simple occlusal patterns of the upper molars in *Hadromys humei* reflect the strong coalescence of the cusps forming each lamina and the absence of a posterolingual cusp (t7), anterolabial cusp (t3), and posterior cingulum from each molar.

These high-crowned upper molars are multirooted (fig. 5). The first molar is anchored by a large anterior root, two lingual roots that are separated throughout their lengths, one moderately large posterior root that is located at the posterolabial margin of the tooth op-

posite the posterior lingual root, and one slim labial root. The basic configuration is four roots in a square set posterior to a large and strong anterior root. The second molar is anchored by a large anterolingual, posterolingual, divided posterolabial, small labial, and large anterolabial roots. The third molar has two large anterior roots, one at each corner of the tooth, a large posterior root, a small lingual, and a small labial.

The lower molars are high-crowned, broad, and also have simple chewing surfaces (fig. 5). Oblong anterolabial and anterolingual cusps form a slanted lamina at the front of the first lower molar. Behind that is a broad and slightly slanted second lamina. The back lamina is chevron shaped. A small cusp, the posterior cingulum, sits on the posterior edge

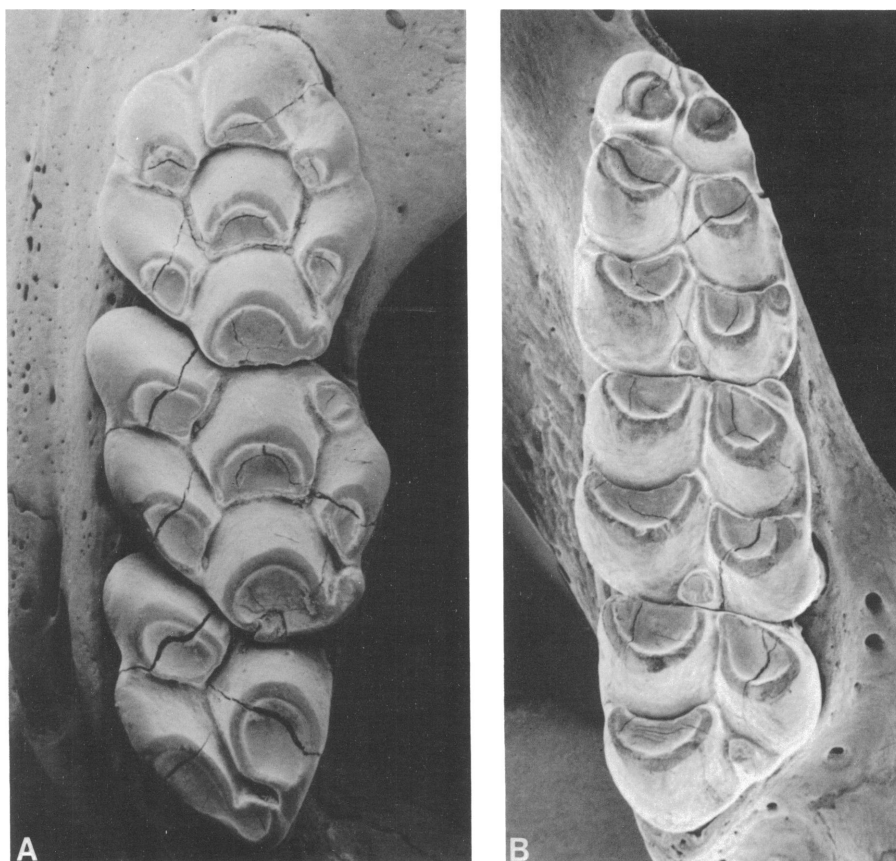


Fig. 6. Molar rows of adult *Golunda ellioti* (AMNH 171133). **A**, left upper molars (CLM1-3 = 6.3 mm). **B**, right lower molars (CLM1-3 = 6.2 mm). Contrast the cusp patterns shown here with those of *Hadromys humei* in figure 5.

of the tooth and is nearly hidden between the first and second molars. Two broad laminae form the occlusal surface of the second molar; the posterior cingulum is larger than the comparable cusp on the first molar. The third molar consists of two simple and straight laminae. A cusplet at the posterolabial margin of the first molar, plus a large anterolabial cusp and small anterior labial cusplet on the second molar, provide a degree of cuspidation to those teeth. The third molar is without either anterolabial cusp or cusplets.

The root pattern of the lower molars is not as complex as that of the uppers. The first lower molar is anchored by a large anterior root, a broad but single posterior root, and a small labial root. The second and third molars are each anchored by three roots: small

anterolabial and anterolingual roots and a large, broad posterior root.

THE PLEISTOCENE SPECIES OF *HADROMYS*

The northeastern margin of the Indian subcontinent contains the small geographic range of living *Hadromys*. The fossil *Hadromys* comes from northern Pakistan at the opposite northwestern edge of the subcontinent. The fossil species is represented by three upper molars; judged by dental wear, each tooth is from a different individual. Dental features support a hypothesis that the teeth are a sample of an extinct species of *Hadromys*, which I name and describe below.

TABLE 2
Measurements (in Millimeters) of Right Upper
Molars in Samples of *Hadromys humei* from India
and *Hadromys loujacobsi* from Pakistan^a

Measure- ment	<i>H. humei</i>	<i>H. loujacobsi</i>	
	Manipur (N = 26) ^b	DP 204	DP 206
CLM1-3	5.62 ± 0.2 (5.4-6.0)		
BM1	1.9 ± 0.1 (1.8-2.0)	2.3	
BM2	1.8 ± 0.1 (1.8-1.9)		2.2
LM1	2.8 ± 0.1 (2.5-3.1)	3.7	
LM2	1.5 ± 0.1 (1.4-1.7)		2.0

^a Abbreviations: CLM, crown length of maxillary molar row; BM, breadth of molar; and LM, length of molar. Crown length of molar row and breadth of molar represent greatest dimensions, usually near bases of molars. Length of molar was taken near the occlusal surface because I could not measure basal dimensions on intact molar rows of the Recent specimens. Statistics are mean plus or minus one standard deviation, and observed range in parentheses.

^b Specimens, which I measured, are from Bishampur, Imphal, and Moirang in Manipur State, India: BM 85.8.1.321, 85.8.1.323, 47.189-47.206, 66.1530-66.1532, and 67.110-67.112. Ages in the sample range from old to young adults.

Hadromys loujacobsi, new species

HOLOTYPE: DP 204, the right first upper molar (figs. 7, 9; also illustrated by Jacobs, 1978: 69) of a young adult. The crown and cusps are complete, basal fragments of the roots are present.

DIAGNOSIS: The Pleistocene *Hadromys loujacobsi* is distinguished from the living *H. humei* by the following dental characters associated with the first and second upper molars (see also table 2 and fig. 7):

1. teeth longer and broader (probably derived conditions);
2. cusps forming first and second laminae of first molar and first lamina of second molar aligned next to one another so they form less arcuate (first molar) or nearly straight (second molar) laminae (derived configurations);
3. cusp t9 of first molar a discrete cone, not a ridge, not fused to cusp t6 in young rats, and larger relative to the adjacent cusp t8; cusp t9 of second molar also not coalesced with cusp t6 in young rats (primitive features);

4. roots fewer beneath first molar and arranged in a primitive pattern.

TYPE LOCALITY: Pabbi (or Kharian) Hills, on the southeastern margin of the Potwar Plateau, in the Punjab region of northern Pakistan.

REFERRED SPECIMENS: DP 205, the left first upper molar from an adult and DP 206, the right second upper molar from either a juvenile or very young adult (figs. 7, 9). DP 205 is incomplete: the posterior half of the back lamina and part of the posterolabial margin of the molar are missing; basal portions of the roots are present. Crown and cusps of DP 206 are intact but there is no sign of roots.

MEASUREMENTS: See table 2.

STRATIGRAPHIC LOCALITY: The holotype and two other specimens are from Locality DP 24 (mapped by Keller et al., 1977, and Jacobs, 1978) in the Upper Siwalik Group. Jacobs (1978) reported that Locality DP 24 is in the Pinjor Zone of the Upper Siwaliks if Pilgrim's terminology is followed, or the Soan Formation according to the Stratigraphic Committee of Pakistan.

AGE: Jacobs (1978: 11) wrote that "DP locality 24 occurs slightly above the Olduvai magnetic event in the Pabbi Hills. It, therefore, is early Pleistocene in age, and younger than about 1.9 m.y." Revised calibration of the paleomagnetic time scale involving the Olduvai Event gives an upper age limit of less than 1.66 m.y. (Lowrie and Alvarez, 1981). Magnetic polarity stratigraphy of the Pabbi Hills is also documented by Keller et al. (1977) and Opdyke et al. (1979).

ETYMOLOGY: I name the Pleistocene *Hadromys* after Dr. Louis L. Jacobs (Shuler Museum, Southern Methodist University) whose studies of the Siwalik fauna, especially murids, has enriched our knowledge about past mammalian evolution and diversity in Central Asia.

DESCRIPTION AND COMPARISONS: Under the identification of "Cf. *Rattus* sp.," Jacobs (1978: 68-70) provided good descriptions of the three isolated molars that I refer to *Hadromys loujacobsi*. As he noted, molars of the Pleistocene species are hypsodont, rooted, and the rows of cusps slant strongly backwards, features that also characterize the living *Hadromys*. The two species also resemble each

other in number of cusps and their general arrangement but differ in alignment and discreteness of particular cusps. In the first molar of *H. loujacobsi*, cusp t1 of the anterior lamina and cusps t4 and t6 of the second lamina are aligned more anterior relative to the central cusp than are the comparable cusps in *H. humei*; the laminae of *H. loujacobsi* are slightly bowed in occlusal view rather than strongly arcuate as they are in *H. humei* (fig. 7). The cusps are also aligned next to each other in the anterior lamina of the second molar of the fossil species so that the lamina, at least in the slightly worn tooth, appears nearly straight, a contrast to the curved front lamina in the second molar of the living rat (fig. 7).

The nature of cusp t9 differs between the Pleistocene and living species. In the first molar of *H. loujacobsi*, cusp t9 is large, columnar, distinct, and directed anteriorly. It is attached to the large central cusp t8 but not to the labial cusp t6 of the lamina in front. Cusps t9 and t6 would coalesce only after the chewing surface became worn down nearly to bases of the cusps. That condition is shown by DP 205; although that first molar is incomplete, enough remains of the labial edge to indicate that the third lamina was strongly united with the second at the labial margin. Cusp t9 in *H. humei*, by contrast, is smaller relative to cusp t8, directed forward and shaped more like a ridge than a columnar cusp, and is fused with cusp t6 even in young adults. The configuration is clearly shown in figure 7 where the youngest specimen of *H. humei* I could locate is illustrated. In the second molar of *H. loujacobsi*, cusp t9 is thin and resembles a ridge stretching from cusp t8 to cusp t6 of the lamina in front (fig. 7), but it would not coalesce with cusp t6 until after appreciable wear. Cusp t9 on the second molar of *H. humei* is a ridge fused with cusp t6, closely similar to the configuration in the first molar.

Specimen DP 204 and DP 206 are examples of molars with little wear of the occlusal surfaces. A worn chewing surface in *H. loujacobsi* is represented by the incomplete DP 205 (fig. 7). The slightly bowed laminae are evident on that specimen.

The two species differ in number and position of roots on the first molar. That tooth

in *H. humei* is anchored by a large anterior root and behind that four small roots, each located at the corner of a square (fig. 5). Four roots anchor the first upper molar of *H. loujacobsi*. A large anterior root is beneath the front of the tooth. Directly opposite this root at the back of the molar is a large posterior root; in *H. humei*, the posterior root is relatively smaller and located at the posterolabial corner of the molar. There is a single, wide lingual root and no indication in either of the fossil molars that the root is divided near its base (clearly shown in the sketch by Jacobs, 1978: 69); two small lingual roots occur in the living species. Finally, opposite the lingual root in *H. loujacobsi* is a small labial root.

Jacobs (1978: 70) noted a difference between the living species of *Hadromys* and his fossil that led him to exclude it from *Hadromys* and instead assign it to cf. *Rattus*. He reported that in *H. humei* the second and third laminae were more broadly connected to each other on both lingual and labial margins than were comparable laminae in the fossil molars. I see no difference between the two species in degree of union of the laminae at their lingual margins, but he is correct about the labial coalescence. The condition of the laminae will have to be reviewed if additional material of both species becomes available, especially younger specimens of the living *Hadromys* in which the teeth are but slightly worn (I could not find such young examples in the museum collections I surveyed).

RELATIONSHIPS

Two aspects need to be explored, neither of which can be pursued here in great depth. One is the nature of the relationship between the living and the Pleistocene species of *Hadromys*, the other is the relationship between *Hadromys* and *Rattus* on the one hand, and *Hadromys* and genera in the arvicanthine group on the other.

My knowledge of *Hadromys loujacobsi* derives from only three isolated upper molars. From their morphology it is clear that the Pleistocene species was slightly larger in body size than the living *Hadromys* but may have had similar habits. The appreciable coronal hypsodonty of *H. loujacobsi* and its broad,

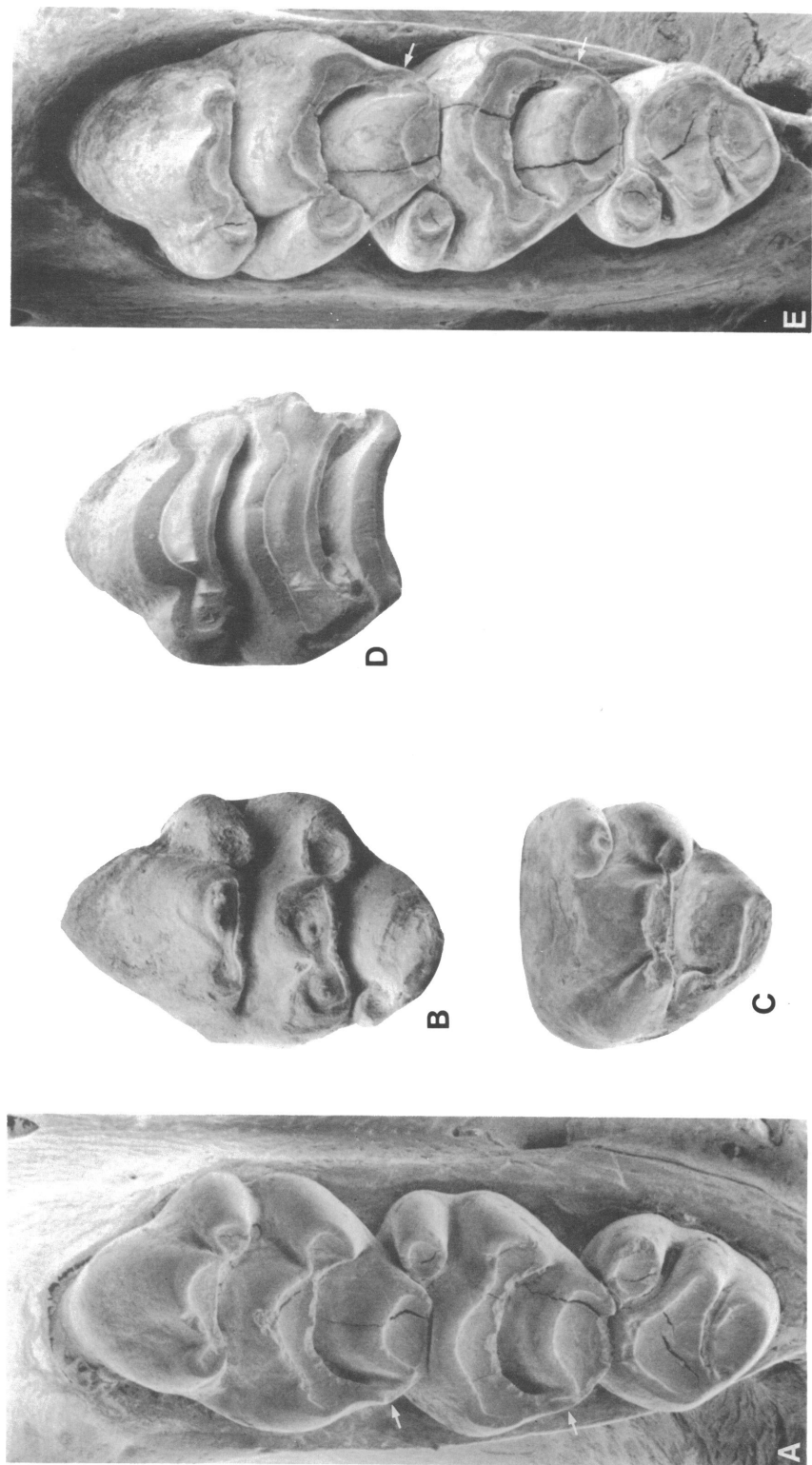


Fig. 7. Upper molars of the living *Hadromys humei* and Pleistocene *H. louiacobsi* compared. A and E, right and left molar rows, respectively, of *H. humei* (FMNH 76567; CLM1-3 = 5.5 mm); arrows point to cusps t9. B-D, *H. louiacobsi* (see measurements in table 2): B, DP 204, holotype, right molar from a very young adult (note the larger, columnar cusp t9 and the slightly bowed laminae); C, DP 206, right second molar of either a very young adult or juvenile (the anterior lamina is nearly straight compared with the arcuate lamina in *H. humei*, and cusp t9 is large, somewhat ridgelike, and not fused with cusp t6); D, DP 205, first left molar of an adult, which is worn more than the molar surfaces in the adjacent *H. humei*.

laminar chewing surfaces suggest that it, like *H. humei*, may have been a grazer. The slightly bowed or nearly straight laminae so characteristic of the fossil species indicate a greater specialization of the occlusal surface than the less derived pattern of the living *Hadromys*.

Other features of *H. loujacobsi*, however, are primitive compared to *H. humei*. The discrete and large cusp t9 on the first upper molar is a primitive configuration compared with the ridgelike cusp t9 that connects the second and third laminae in the first molar of *H. humei*. Three roots beneath the first upper molar—a large anterior, lingual, and posterior—is primitive in murine rodents (Musser and Newcomb, 1983). *Hadromys loujacobsi* has those three roots, all primitively situated, but also has a small labial root, which is a derivation relative to the primitive configuration. However, the fossil species is more primitive than *H. humei* because that species has five roots, the lingual root is divided into two roots, and the posterior root is at the posterolabial margin of the tooth instead of at the back (fig. 5).

Hadromys loujacobsi is slightly larger than *H. humei*, its laminar occlusal surface is more specialized, but in distinctness of cusp t9 and anchorage of first upper molars, the Pleistocene species is slightly more primitive than the living *Hadromys*. Without other molars, incisors, skull, or postcranial skeleton of the fossil, little more can be stated about relationships between *H. loujacobsi* and *H. humei*. Other than *H. humei*, I know of no other described living or fossil murine whose upper molars resemble those of the three from the Siwaliks. The high crowns, steeply inclined rows of cusps, and patterns formed by those cusps in the fossil are morphologically closest to *H. humei*. Coronal hypsodonty, appreciable inclination of cusp rows, overlap of molars, and coalescence of most cusps to form laminae are derived features within murines.

That *H. loujacobsi* is less derived in some dental traits than *H. humei* may or may not go along with its antiquity. Fossils of *H. humei* are unknown; its history may go back into the Pleistocene or earlier. Because the fragmentary material of *H. loujacobsi* exhibits a few more primitive than derived traits relative to the living *Hadromys* does not mean

that the Pleistocene species was ancestral to *H. humei*. The evidence indicates only that *H. loujacobsi* and *H. humei* are sister species probably derived from the same ancestral stock.

I compared the three molars of *H. loujacobsi* with species of *Rattus* and also with samples of *Golunda*, *Mylomys*, *Pelomys*, *Lemniscomys*, *Rhabdomys*, and *Arvicanthis*, genera that are thought to cluster in what has been called an Arvicanthine Division (Misonne, 1969); some of these forms have been associated with *Hadromys*. The link between the fossils and *Rattus* simply reflects the simple cuspidation that characterizes many genera of murines and does not indicate close phylogenetic relationships. The coronal hypsodonty, anteriorly positioned cusp t9, and number of roots beneath the first upper molar are features outside the range of dental variation within *Rattus* (Musser, 1982; Musser and Newcomb, 1983).

Phylogenetic ties between *Hadromys* and other described murine rodents are obscure. When he named and diagnosed *Hadromys*, Thomas (1886b: 999) noted that "its resemblance, both external and cranial, to *Golunda* is very striking." Ellerman (1941: 127) first suggested that *Hadromys* was "by no means easily distinguished generically from *Arvicanthis*," but then wrote (Ellerman, 1946) that *Hadromys* and *Golunda* were probably derived from the same stock, and in 1961 (p. 714) he suspected that *Hadromys* "might be related to *Golunda*, although it is very much less extreme dentally than that." By 1969, Misonne's study of evolutionary trends in African and Indo-Australian Muridae was published and there he wrote that the relict *Hadromys* was a distinct genus belonging in what he defined as an "Arvicanthine Division." Along with *Arvicanthis* and *Hadromys*, Misonne included *Aethomys*, *Bandicota*, *Dasyomys*, *Dephomys*, *Golunda*, *Hybomys*, *Lemniscomys*, *Mylomys*, *Nesokia*, *Pelomys*, *Rhabdomys*, and *Stochomys* in this group. *Hadromys*, Misonne noted (p. 116), "seems to be closest to *Golunda*, *Dasyomys* and *Arvicanthis*, but these genera are more advanced than it, and hence a direct comparison is difficult."

Misonne defined the Arvicanthine Division by dental traits and his observations will

have to be tested by data from other sets of characters. My studies of species in this group, even using only dentitions, lead me to conclude that *Aethomys*, *Hybomys*, *Dephomys*, *Stochomys*, *Nesokia*, *Bandicota*, and probably *Dasymys* are not members of the arvicanthine cluster; even Misonne (1969: 116) was uncertain about including *Nesokia* and *Bandicota*. The residue—*Arvicanthis*, *Pelomys*, *Mylomys*, *Rhabdomys*, *Lemniscomys*, and possibly *Golunda*—can be grouped using a combination of derived external, dental, and cranial traits; it is this cluster that I will refer to in my comparisons below between *Hadromys* and arvicanthines.

Whether or not *Hadromys* is closely related to arvicanthines can be determined only by analyses of as many characters as possible among the species. Results from such a study are not yet available. My preliminary observations suggest that although *Hadromys* has body and tail proportions similar to arvicanthines, a long and narrow hind foot with short outer digits, similar cranial and mandibular conformations, and a multiplication of molar roots, the two species may not be especially closely related to species in the *Arvicanthis* Division. *Hadromys humei* has more primitive structures than living arvicanthines: it retains a wide and prominent alisphenoid strut, which is absent in species of *Arvicanthis*, *Pelomys*, *Mylomys*, *Lemniscomys*, *Rhabdomys*, and *Golunda*. *Hadromys* has smaller auditory bullae relative to cranial size than do arvicanthines, all of which have bullae that are inflated to some degree; relatively small bullae is primitive.

Hadromys is more specialized than the other genera in several cranial features. Compared with arvicanthines, the Indian rat has a shorter and broader rostrum relative to the rest of the cranium. The breadth partly reflects the wide premaxillae, which are wider relative to the nasal breadth (in dorsal view) than in any species of arvicanthine. *Hadromys* also has a more specialized zygomatic plate. The anterior spine extends forward so far that it covers the opening of the nasolacrimal capsule, and the anterior margin of the spine is deeply concave. In *Arvicanthis* and its relatives, the zygomatic spine extends anteriorly only to the back of the nasolacrimal capsule, and the anterior margin is straight

or slightly concave in all genera. Another derived trait in *Hadromys* is its threadlike pterygoid bridge; in arvicanthines the bridge is stronger and is a wide, shelflike extension of the pterygoid ridge.

Molars, especially the uppers, in both species of *Hadromys* are derived compared with those in arvicanthines. The latter have highly cuspidate upper teeth that retain their cuspidate nature even after appreciable wear; none of the species have either the arcuate or slightly bowed laminar patterns seen in the fossil and living species of *Hadromys* (compare figs. 5 and 7 with fig. 8). An occlusal pattern in which the cusps are coalesced to form laminae, whether arcuate or nearly straight, is specialized compared with occlusal surfaces formed of rows of discrete cusps. The anterior portion of the first lower molar in *Hadromys* is also laminar and results from the fusion of oblong anterolabial and anterolingual cusps; furthermore, the lamina is not straight but slants toward the posterolabial side (fig. 5). This configuration is specialized and unlike any of the conformations seen in species of living arvicanthines (see the illustrations in Misonne, 1969) where the lamina consists of either two discrete cusps (most species) or three (*Rhabdomys*).

The striking coronal hypsodonty seen in *Hadromys*, also a specialization, does not occur in any arvicanthine; molars have very low crowns in those species, a primitive condition. The contrast in crown height between *Hadromys humei* and *Pelomys minor* that is illustrated in figure 9 is typical of the difference between *Hadromys* and all the other species of arvicanthines.

Finally, in both *Hadromys* and the arvicanthine genera the first upper and lower molars are anchored by multiple roots—more than the primitive number (three under the upper, two beneath the lower). *Hadromys*, however, is not as specialized as the other genera because it does not have a lingual root on the first lower molar; a strong lingual root, in addition to the anterior, posterior, and labial roots, is present beneath the first lower molar in all species of arvicanthines I examined.

One genus in the *Arvicanthis* Division, *Golunda*, has repeatedly been linked phylogenetically to *Hadromys* (Thomas, 1886a,

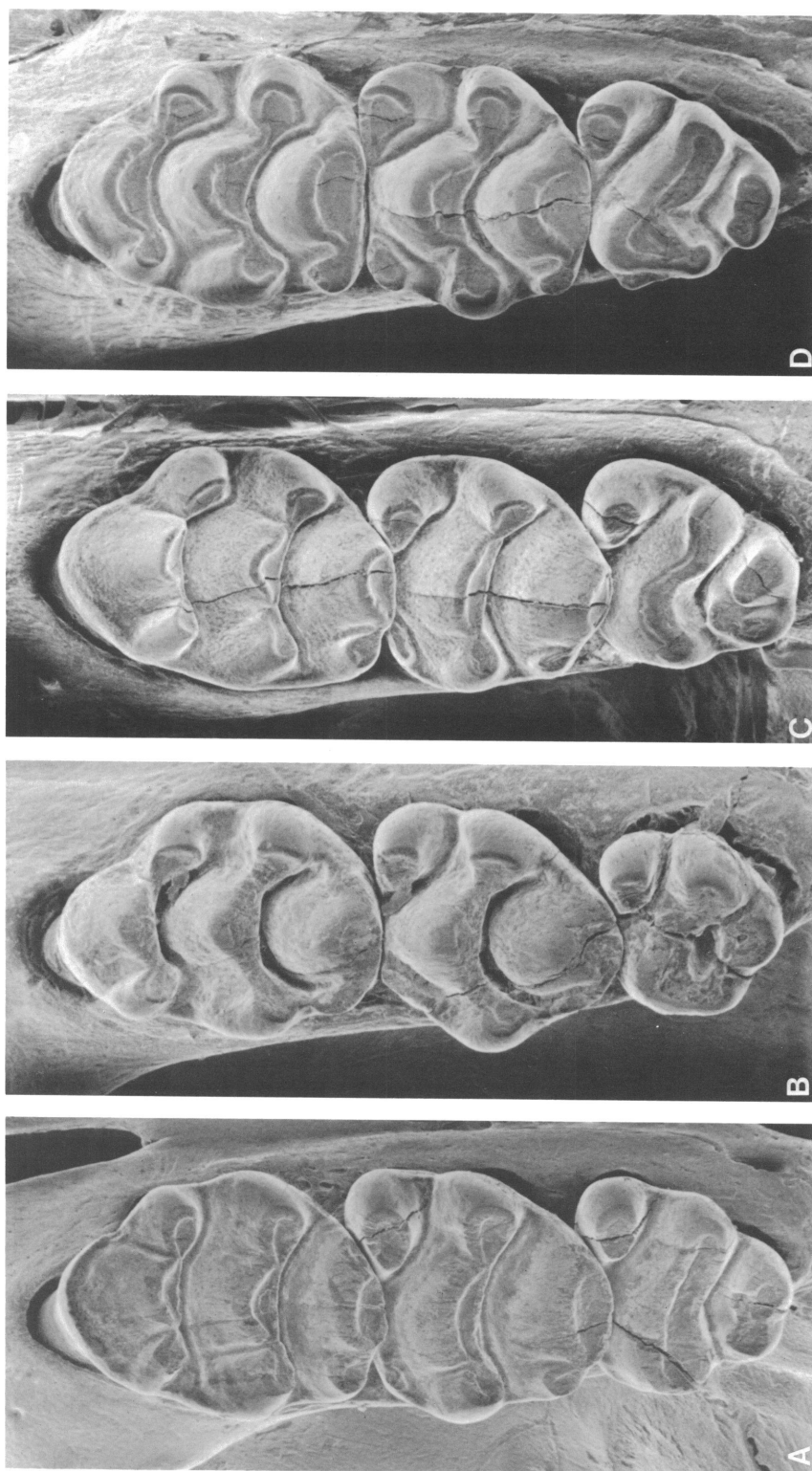


Fig. 8. Young adult right upper molar rows in species of the *Arvicanthis* Division. A, *Rhabdomys pumilio* (AMNH 162190; CLM1-3 = 4.5 mm). B, *Lenniscoomys griselda* (AMNH 55199; CLM1-3 = 5.0 mm). Note how similar the cusp patterns are among the four species and how different they are contrasted with occlusal patterns in *Hadromys humei* and *H. lowiacobsi* (fig. 7).

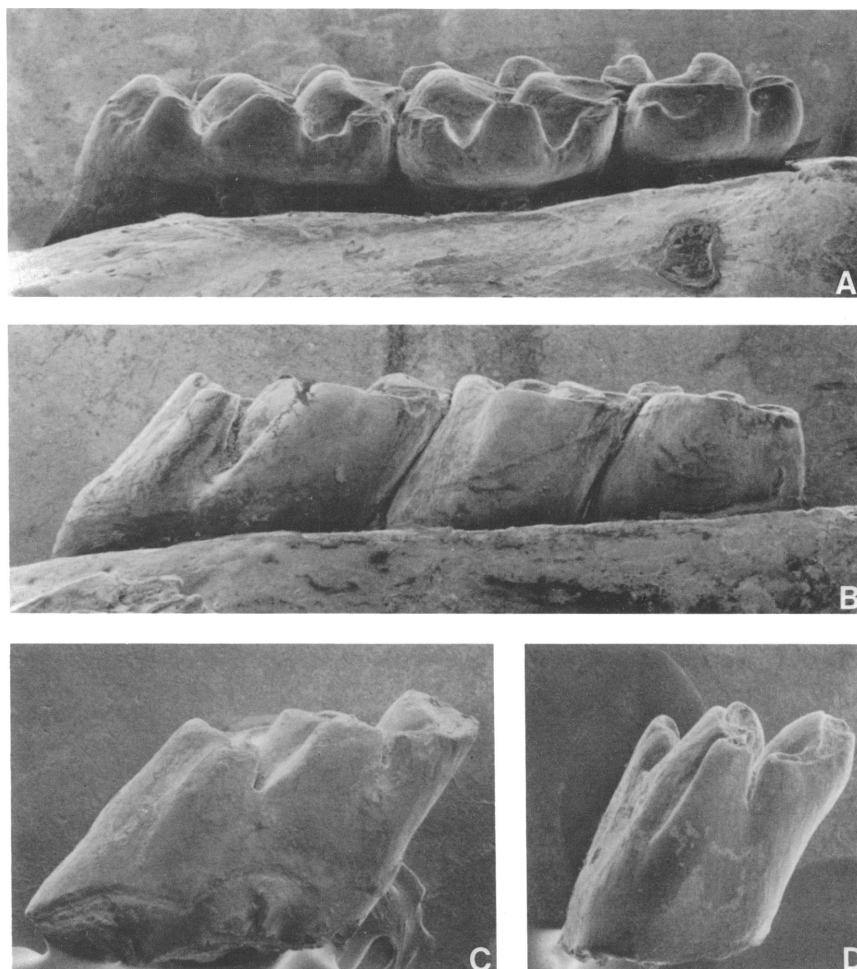


Fig. 9. Contrast between hypsodont and brachydont upper molars. The coronal hypsodonty of *Hadromys humei* (B; FMNH 76567; CLM1-3 = 5.5 mm) is very similar to the first (C; DP 204, holotype) and second (D; DP 206) molars of *Hadromys loujacobsi*. Both of these species contrast sharply with the low-crowned molars of *Pelomys minor* (A; AMNH 86122; CLM1-3 = 5.2 mm). Brachydonty is typical in species of genera in the *Arvicanthis* Division (*Arvicanthis*, *Pelomys*, *Lemniscomys*, *Rhabdomys*, *Myiomys*, *Golunda*, and *Dasymys*).

1886b; Ellerman, 1946, 1961; Misonne, 1969). *Golunda ellioti* is the sole living species and is native to the Indian subcontinent where it has been recorded from Sri Lanka and on peninsular India northward to Gujarat, southern Rajasthan, the Punjab, Pakistan, Kashmir, Nepal, and Bhutan (Ellerman, 1961; Ellerman and Morrison-Scott, 1951; Roberts, 1977). The range extends to northeastern India at Angarakhata in Kamrup District where it overlaps with the geographic distribution of *Hadromys humei* (a specimen of

H. humei was collected at 300 ft, one *G. ellioti* was obtained at 600 ft elevation; Hinton and Lindsay, 1926). Other than the shared arvicanthine body proportions and general skull conformation, I cannot find characters that would closely tie *Hadromys* phylogenetically to *Golunda*. The latter has grooved upper incisors, *Hadromys* does not, and the occlusal patterns of upper and lower molars are nothing like those in *Hadromys* (compare figs. 5 and 6). All other traits seen in teeth and skulls of *Golunda* are either unique or shared

with some or all (depending on the combination of features) of the African arvicanthine genera and not with *Hadromys*.

Preliminary results of my studies make me skeptical about including *Hadromys* within Misonne's *Arvicanthis* Division. The arvicanthine gestalt of head, body, tail, and skull shapes and proportions is the primary reason for placing *Hadromys* with arvicanthines, but these features are strongly associated with many murines living in grassland habitats and could have evolved independently. Dental traits characterizing both species of *Hadromys* are not shared by any species of *Arvicanthis* and related genera. Perhaps the best hypothesis now available on phylogenetic affinities is to consider the species of *Hadromys* to have been derived from some late Miocene ancestor, a species of *Karnimata*, for example. Such a notion was suggested by Jacobs (1978) to explain the origin of the species represented by the three molars he identified as cf. *Rattus* sp. and which I described as *H. loujacobsi*.

FAUNAL AND HABITAT ASSOCIATIONS

Fossilized remains of other murines in addition to *Hadromys loujacobsi* have been found at Locality DP 24 in the Pabbi Hills. *Golunda kelleri* is represented by an isolated upper incisor fragment and several lower molars; a species of *Mus* is known from one upper and two lower molars; and a third species, considered to be unidentifiable by Jacobs (1978), is indicated by a second upper molar and a first lower molar.

Dental traits of *Golunda kelleri* (see the illustrations in Jacobs, 1978: 65) are closely similar to those of the living *G. ellioti*, which occurs in northern Pakistan today (Roberts, 1977). For Jacobs, the primary distinctions between the Pleistocene and living species are that *G. kelleri* lacks a posterior labial cusplet (cusp C1 in his terminology) on the first lower molar, and the large posterior cusp (Jacobs called this the hypoconid) forming the back of the third lower molar is situated slightly more to the labial side rather than directly on the lingual side as is the configuration in *G. ellioti*. On excellent casts of the Siwalik

specimens in front of me, there is a small posterior labial cusplet on the first molar that is plastered against the hypoconid; it is not as large and conspicuous as the comparable cusplet in samples of *G. ellioti* but present nevertheless. Size of the posterior labial cusplet is variable in samples of *G. ellioti*. It may be a large conspicuous cusp as in AMNH 171133 (fig. 6) from the Punjab of India, or indistinct, as it is in AMNH 240858 from Sri Lanka. The size and distinctness of the cusplet in the latter is very similar to those qualities of the cusplet in *G. kelleri*. The contrast between the fossil and living species in relative position of the posterior cusp on the third molar is evident in the small samples I examined and may be the only feature of the lower molars that sets *G. kelleri* apart from *G. ellioti*; the distribution of that character, however, should be checked in samples of *G. ellioti* from throughout its geographic range.

Molar characters of the *Mus* are more like *Mus booduga*, which is part of the modern Pakistan fauna (Roberts, 1977), than any other species of *Mus* living in the region, according to Jacobs (1978; see the illustrations of teeth on p. 44). I have studied casts of the fossils and I agree with him; the Pleistocene molars are larger than those of any specimen of *M. booduga* I examined, but conformation of their cusp patterns and degree to which the cusp rows incline are very similar to *M. booduga*. Whatever species the fossilized molars represent, the characters of the teeth indicate that species to be a member of subgenus *Mus* and not one of the several other subgenera now placed in the genus (Marshall, 1977).

The simple cusp patterns of the two molars representing the third species in the Pabbi Hills fauna were unfamiliar to Jacobs (1978). I have compared the two specimens (not casts) with samples of native Indian murines and they come closest to *Millardia*. Although both are much smaller than those of any living species of that genus and have their own distinctive features, they somewhat resemble dental traits in my sample of *Millardia kathleenae*. Both molars could be from the same species.

Flynn and Jacobs (1982: 136) asserted that "Advanced *Mus* and the modern genus *Go-*

lunda, without rhizomyids, may be considered indicative of Pleistocene age in the Potwar Plateau." This composition of species may represent the culmination of faunal changes over about 13 million years in the region, which reflects increasing aridity and replacement of forest by scrub and grassland. To this Pleistocene association should be added *Hadromys*.

Habitats in Pakistan during the Pleistocene and now may not have been too different. Roberts (1977) has characterized the Potwar Plateau and Pabbi Hills region as Arid Subtropical Habitat with a slight monsoon influence. Summers are dry and hot, frost is usual during winters but showers are irregular. Low tropical thorn scrub on rocky and hilly countryside is the vegetative association. *Acacia modesta*, *Olea cuspidata*, and *Tecomella undulata* are the common shrubs. *Golunda ellioti* occurs here and also in adjacent areas where the summers are humid and mild, the winters dry. According to Roberts (1977: 267), *G. ellioti* "is found in relatively barren regions provided there is some growth of tropical thorn scrub or grass clumps and it seems to favour rocky tracts rather than cultivated valley bottoms." The animal shelters among rock crevices and sometimes uses burrows dug by other animals. It uses runways through grass and cover provided by bushes and rock overhangs. *Mus booduga*, reported Roberts (1977), inhabits cropland and patches of tropical thorn scrub adjacent to cultivated fields. It is also found on rocky hillsides but not much higher than 2000 ft. *Golunda ellioti* and *Mus booduga* are closely similar in dental characters to the Pleistocene *Golunda kelleri* and *Mus* sp. Populations of these species probably occurred in low scrubby forest and grassland, a habitat that would also have accommodated *Hadromys loujacobsi*.

Five other species of murids, in addition to *Golunda ellioti* and *Mus booduga*, live today in the Potwar Plateau and Pabbi Hills region (table 3). Most of these are primarily terrestrial, although *Golunda ellioti* and some *Mus* do climb about in low shrubs (Roberts, 1977); *Nesokia indica* is one of the most fossorial of murines; and *Rattus rattus* is the only one that is as agile in trees and shrubs as on the ground. The small number of species coupled with the generally arid climate and

scrubby habitat of the region in northern Pakistan contrast sharply with the number and composition of the murid fauna in Manipur, the wetter tropical climate, and the more diverse range of habitats.

In Manipur State, the fauna associated with *Hadromys humei* occurs between 2600 and 4000 ft; frost line is about 3000 ft (Roonwal, 1949). Summers are cool, reaching a high of about 92°F; winters are cold but not severe, descending to 30°F. Average annual rainfall at Imphal is 70 in., most of it falling in the monsoon months from June to September. Several major habitats are found in the region: oak scrub; oak parkland; tropical lowland evergreen rain forest; and riverine habitats of scrub, meadow, and climax gallery forest. Roonwal (1949) has provided descriptions of these habitats. Fifteen species of murids are known from the Manipur region (table 3). Some are primarily terrestrial (*Berylmys*, for example), others are both terrestrial and arboreal (*Rattus*), and *Chiropodomys gliroides* is highly specialized for arboreal life. Among these, only *Mus musculus*, *Bandicota bengalensis*, and *Rattus rattus* are common to Manipur and the Potwar Plateau and Pabbi Hills; however, the samples of the house rat represent different populations (table 3).

This is a superficial picture of murid faunas at the opposite edges of the northern Indian subcontinent but it does illustrate general differences in climate as well as species and habitat diversities. *Hadromys humei* is part of a fauna associated with tropical and subtropical monsoon habitats. Whether this was the Potwar climate as far back as the early Pleistocene is unknown. *Hadromys loujacobsi* may have been part of a faunal assemblage adapted to habitats reflecting greater aridity. The picture is simplistic, possibly incorrect. Past geographic distributions of either species of *Hadromys* is as unknown as is the full contemporary extent of the range of *H. humei*.

BIOGEOGRAPHY

Hadromys humei and the other species of murids occurring in Manipur State are native to Asia. Of these, *H. humei* and *Diomys crumpi* have small geographic ranges apparently confined to northeastern India, south-

eastern Nepal, and nearby Burma (this report; Ellerman, 1961; Ingles et al., 1980; Musser and Newcomb, 1983). *Bandicota bengalensis* is widespread over the Indian subcontinent and has also been recorded from the islands of Penang, Sumatra, and Java on the Sunda Shelf where they were likely introduced through human agency (Ellerman, 1961; Musser and Newcomb, 1983). *Mus cervicolor* is native to the northern part of the Indian subcontinent from Pakistan (Roberts, 1977) to Burma and also ranges through Indochina; it too has been found on Sumatra and Java and was probably introduced (Marshall, 1977; Musser and Newcomb, 1983). The most expansive portions of the geographic ranges of *Mus cookii*, *Rattus nitidus*, *Rattus sikkimensis*, *Chiropodomys gliroides*, *Niviventer* sp., *Leopoldamys edwardsi*, and species of *Berylmys* are in Indochina; distributions of a few extend onto the Sunda Shelf (Musser, 1979, 1981; Musser and Newcomb, 1983; Musser and Heaney, 1985). *Mus musculus* and the Asian variety of *Rattus rattus* also occur east of continental Asia in parts of the Indo-Australian region where they were likely introduced from mainland Asian sources; some populations of *R. nitidus* are scattered on islands between the Sunda Shelf and New Guinea (Musser, 1977).

Murines of northern Pakistan in the Potwar Plateau and Pabbi Hills region (table 3) are also native Asians. All but two of the living species are found on the Indian subcontinent (Ellerman, 1961; Marshall, 1977). The original range of *Mus musculus* is unknown, although it was most likely Asian. The Indian *Rattus rattus* (see table 3) has extended its range through human activity to many parts of the world; it was probably originally native to the Indian subcontinent (Niethammer, 1975).

The four species represented by isolated teeth from Upper Siwalik sediments in the Pabbi Hills are related to native Indian murids. The dental morphology that Jacobs (1978) attributed to cf. *Rattus* sp. defines a distinctive species of *Hadromys*. *Golunda kelleri*, judged by characteristics of an upper incisor and some lower molars, is closely related to the living *G. ellioti*. Dental traits of the Pleistocene *Mus* resemble the Indian *M. booduga*. Two isolated molars may be from

TABLE 3
Living and Pleistocene Murine Fauna of Potwar Plateau and Pabbi Hills in Northern Pakistan, and Manipur State in Northeastern India

Potwar Plateau and Pabbi Hills ^a	Manipur ^b
Living species	
<i>Mus musculus</i>	<i>Mus musculus</i>
<i>Mus booduga</i>	<i>Mus cookii</i>
	<i>Mus cervicolor</i>
<i>Rattus rattus</i> ^c	<i>Rattus rattus</i>
	<i>Rattus nitidus</i>
	<i>Rattus sikkimensis</i>
<i>Bandicota bengalensis</i>	<i>Bandicota bengalensis</i>
<i>Nesokia indica</i>	
<i>Millardia meltada</i>	
<i>Golunda ellioti</i>	
	<i>Hadromys humei</i>
	<i>Diomys crumpi</i>
	<i>Chiropodomys gliroides</i>
	<i>Niviventer</i> sp.
	<i>Leopoldamys edwardsi</i>
	<i>Berylmys manipulus</i>
	<i>Berylmys bowersii</i>
	<i>Berylmys mackenziei</i>
Pleistocene species	
<i>Mus</i> sp.	
<i>Golunda kelleri</i>	
<i>Hadromys loujacobsi</i>	
? <i>Millardia</i> sp.	

^a The list of species is taken from Roberts (1977).

^b The list is derived from Marshall (1977), Musser (1979, 1981), Musser and Newcomb (1983), and my unpublished records filed in the Department of Mammalogy at the American Museum of Natural History.

^c Samples of *Rattus rattus* from northern Pakistan and Manipur State are from different populations and may not even represent the same species. The Pakistan population is referred to as Oceanian, black, or European house rats, the Manipur population as Asian house rats. The two kinds differ in body and tail proportions, pelage, chromosomal features, and serum transferring patterns (Musser and Calafia, 1982: 10).

a species of *Millardia*. None of the traits that are diagnostic for each of these three taxa

define any other fossil species that has been described from either the Indian subcontinent or places outside of that region.

Present data derived from samples of living murines in northern Pakistan and north-eastern India indicate all are native to Asia, even those that are now distributed worldwide, such as *Mus musculus* and Asian *Rattus rattus*. Species represented by early Pleistocene fossils from the Pabbi Hills are also Asian and apparently native to the Indian region, a hypothesis I accept until it can be falsified by samples from outside of the Indian subcontinent. If the species are indigenous to Asia, what are the zoogeographic relationships indicated by genera? The genera reflect a pattern of affinities very similar to that indicated by the species.

Hadromys

No evidence from samples of either species of *Hadromys* suggests the genus to be anything other than an endemic of the Indian region. Ties to the African genera in the *Arvicanthis* Division have been proposed (Misonne, 1969, for example) but the shared specialized characters may reflect independent adaptation to grassland and savanna habitats and, at best, indicate separate evolution since, presumably, the late Miocene; extensive homoplasy is characteristic of muroid rodents (Carleton and Musser, 1984). Affinities between Indian *Hadromys* and African arvicanthines have been based mostly on dental characters but, as I explained in a previous section, the molar specializations seen in *Hadromys* are not shared by *Arvicanthis* and its allies. What the precise nature of phylogenetic relationships might be between *Hadromys* and members of the *Arvicanthis* Division awaits careful comparative study of not only dental traits but characters of the skull, skeleton, and other systems.

Golunda

Golunda, as defined by *G. kelleri* and *G. ellioti*, is also a native of the Indian subcontinent. Unlike *Hadromys*, however, *Golunda* is thought to be most closely related to the African arvicanthine *Mylomys* and to be represented in Ethiopia by samples from Pliocene strata.

Derived characters reported to be shared by *Mylomys* and *Golunda* include the arvicanthine conformations of body, tail, and hind feet as well as skull shape. Both have grooved upper incisors and similar molar cusp patterns (fig. 10), configurations that, except for third molars, somewhat resemble those in African *Pelomys* (Misonne, 1969; Jacobs, 1978), especially the Ethiopian *P. harringtoni* (Wesselman, 1984). Each third upper molar of *Golunda* has a very derived occlusal surface. The anterolingual-posterior axis of the tooth is elongate, strikingly so compared with the usual murine configuration of other arvicanthine genera (compare fig. 6 with fig. 8). The cusps are inclined, cusp t1 is large and columnar, and the rest of the chewing surface is composed of huge cusps t4 and t5, which are independent and not connected to form a chevron-shaped lamina as they do in *Pelomys*. At the back of the molar is a columnar cusp t8 connected to cusp t5 by a very small round or ridgelike cusp t9. (In first and second upper molars, cusp t9 is oriented toward and sometimes joins cusp t6 of the second cusp row but there is no cusp t6 on the third molar.) To Jacobs (1978: 86), cusp patterns of third molars in *Mylomys* are closely similar to those in *Golunda* and the molar "morphology observed in *Mylomys* and *Golunda* is a shared, derived character and indicates a closer relationship between the Asian *Golunda* and African *Mylomys* than between the African forms *Mylomys* and *Pelomys*. Alternatively, *Golunda* and *Mylomys* may have evolved independently, but in parallel, from a *Pelomys*-like stock."

Cusp patterns are generally similar in *Golunda* and *Mylomys*; however, the resemblance is not so close in details of dental morphology (fig. 10). The African genus contrasts with *Golunda* in the following ways:

1. in each upper molar, cusp t1 is vertical or nearly so and the occlusal surface is oriented at right angles to the anterior-posterior axis of the toothrow (in *Golunda*, cusp t1 on each molar is large and round, somewhat columnar, and slants back at the same inclination as the other lingual cusps);
2. cusps t3 and t9 on the second molar are

- small relative to area of the tooth (relatively larger in *Golunda*);
3. the anterolingual region of the second molar is not stretched so as to appear to be a distorted version of the configuration in *Pelomys*, rather the proportions are closely similar to that genus (in *Golunda*, this region of the molar, particularly cusp t1, is stretched anterolingually so the tooth appears distorted in occlusal view);
 4. the anterolingual cusp and margin of the third molar is not stretched and does not appear distorted relative to the configuration of that molar in *Pelomys*, and is composed of a vertical small cusp t1, which forms the undistorted anterolingual margin, a flattened cusp t4, a large round cusp t5, and a small and round cusp t8 at the back (the anterolingual cusp t1 and margin is stretched toward the front and lingual side, and appears distorted compared with the configuration in either *Mylomys* or *Pelomys*—and there is a small cusp t9 connecting cusps t8 and t5);
 5. cusps forming the anterior lamina on the first lower molar are small relative to the rest of the tooth, the lamina they form is nearly horizontal and only slightly slanted towards the labial side, and each cusp narrows medially—appearing somewhat tear-dropped shape in occlusal view—and in later stages of wear the cusps fuse along their posterior margins (cusps are relatively larger in *Golunda*, the lamina they form slants posterolabially, and each cusp is columnar and in worn teeth fuse along their anterior margins);
 6. no anterocentral cusp on the first lower molar (an anterocentral cusp is present in *Golunda*);
 7. the anteromedial portion of each crescentic entoconid on lower molars is stretched anteriorly (cusps are without a medial sharp elongation in *Golunda*);
 8. there is a large lingual notch between first and second molars and second and third molars but the teeth are flush elsewhere (except for slight notches on lingual and labial sides, molars in *Golunda* are flush

along the surfaces where they touch one another);

9. a posterior labial cusplet is absent from the first lower molar, the anterolabial cusp on the second molar is small and obliterated early in wear, and there is no evidence of cingular labial structures (in *Golunda*, there is a large and conspicuous posterior labial cusplet on the first molar, a well-defined anterolabial cusp on the second, and remnants of labial cingular ridges on the first and second molars);
10. on the third molar, the hypoconid is either absent or a tiny mound or ridge (present as a small cusp in *Golunda*);
11. there is a small labial root in addition to the other roots anchoring the second lower molar (not present in *Golunda*).

Although the crescentic configuration of each cusp is exaggerated in *Mylomys*, as it is in *Golunda*, the overall molar shape and cusp position relative to one another recall those conformations in *Pelomys* and other African arvicanthines rather than that characteristic of *Golunda*. The vertical orientation of the anterolingual cusp (t1) on each upper molar is very similar to the position of comparable cusps in *Pelomys* and other African arvicanthines and is primitive compared with the specialized strongly inclined anterolingual cusps in *Golunda*. The shape of the second upper molar in *Mylomys* is closely similar to that in *Pelomys* and unlike the derived molar in *Golunda* with its elongation along a posterior-anteterolingual axis. Even the third upper molar of *Mylomys*, thought to be so derived and like the molar in *Golunda*, contrasts with that Asian genus in conformation. In *Mylomys*, cusps t1 and t4 are near replicas in size, shape, and position of comparable cusps on the second molar; cusp t5 is larger than t5 on the second molar and cusp t8 is smaller (fig. 10). The tooth is not stretched along an anterolingual-posterior axis. In *Golunda*, cusp t4 on the third molar is not a replica of cusp t4 on the second molar but is a stretched version and cusp t5 is only slightly larger than the comparable cusp on the second molar. Finally, cusp t9 is absent in specimens of *Mylomys* I examined but present as

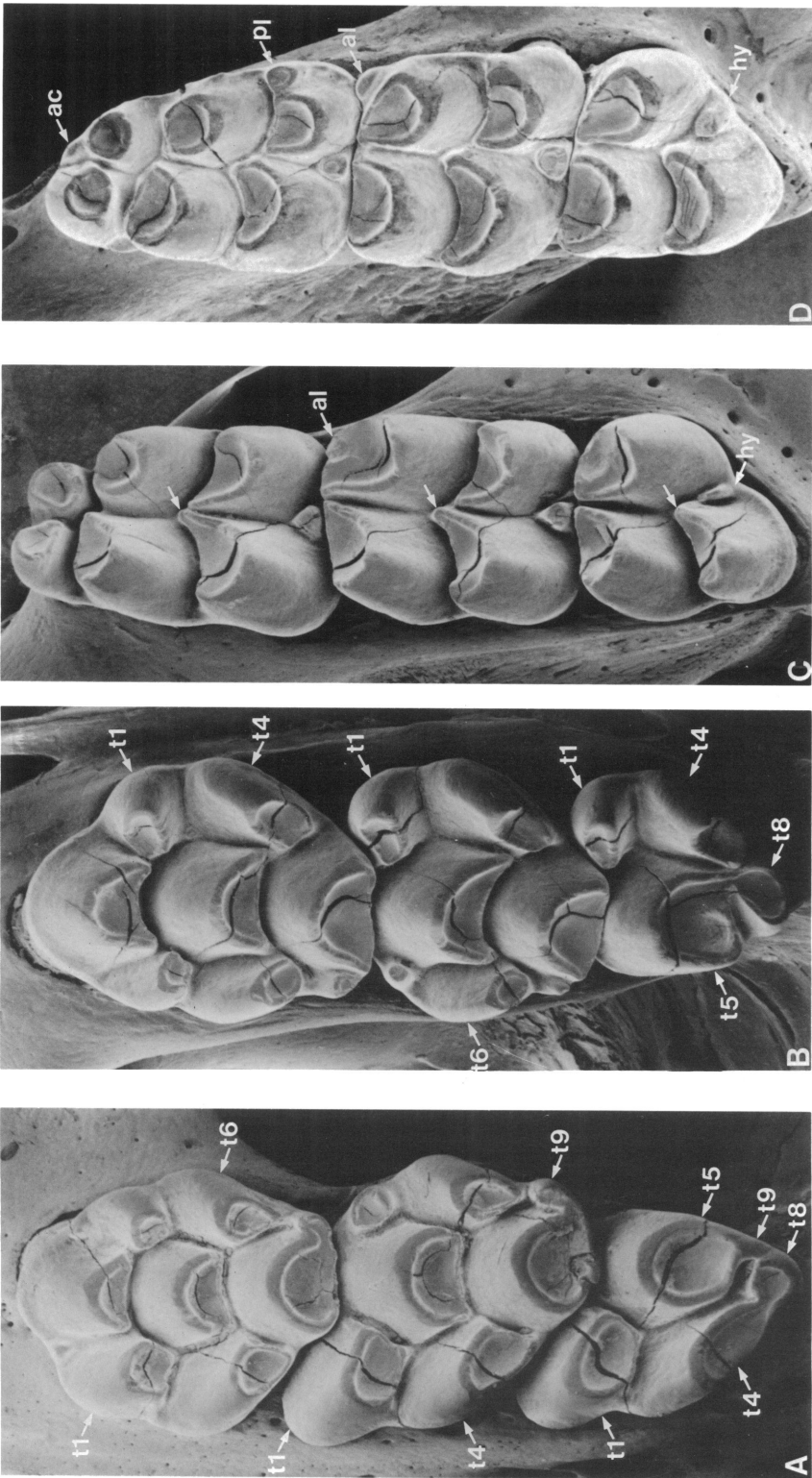


Fig. 10. Young adult molar rows of *Golunda* (AMNH 171133) and *Mylomys* (AMNH 50129). A, left upper molars (CLM1-3 = 6.3 mm) and D, right lower molars (CLM1-3 = 6.2 mm) of *G. ellioti*. B and C, right upper (CLM1-3 = 7.7 mm) and right lower molars (CLM1-3 = 7.7 mm), respectively, of *M. dybowskii*. Note the differences between the two species in shape and orientation of cusps on upper molars, particularly cusp t1, other lingual cusps and the labial cusps, and shape and details of cusp patterns on third molars. Unlabeled arrows in C point to the anteromedial extension of the entoconid; other labeled features are the anteroconid (ac), anterolabial cusps (al), posterior labial cusplet (pl), and hypoconid (hy). Comparisons are discussed in the text.

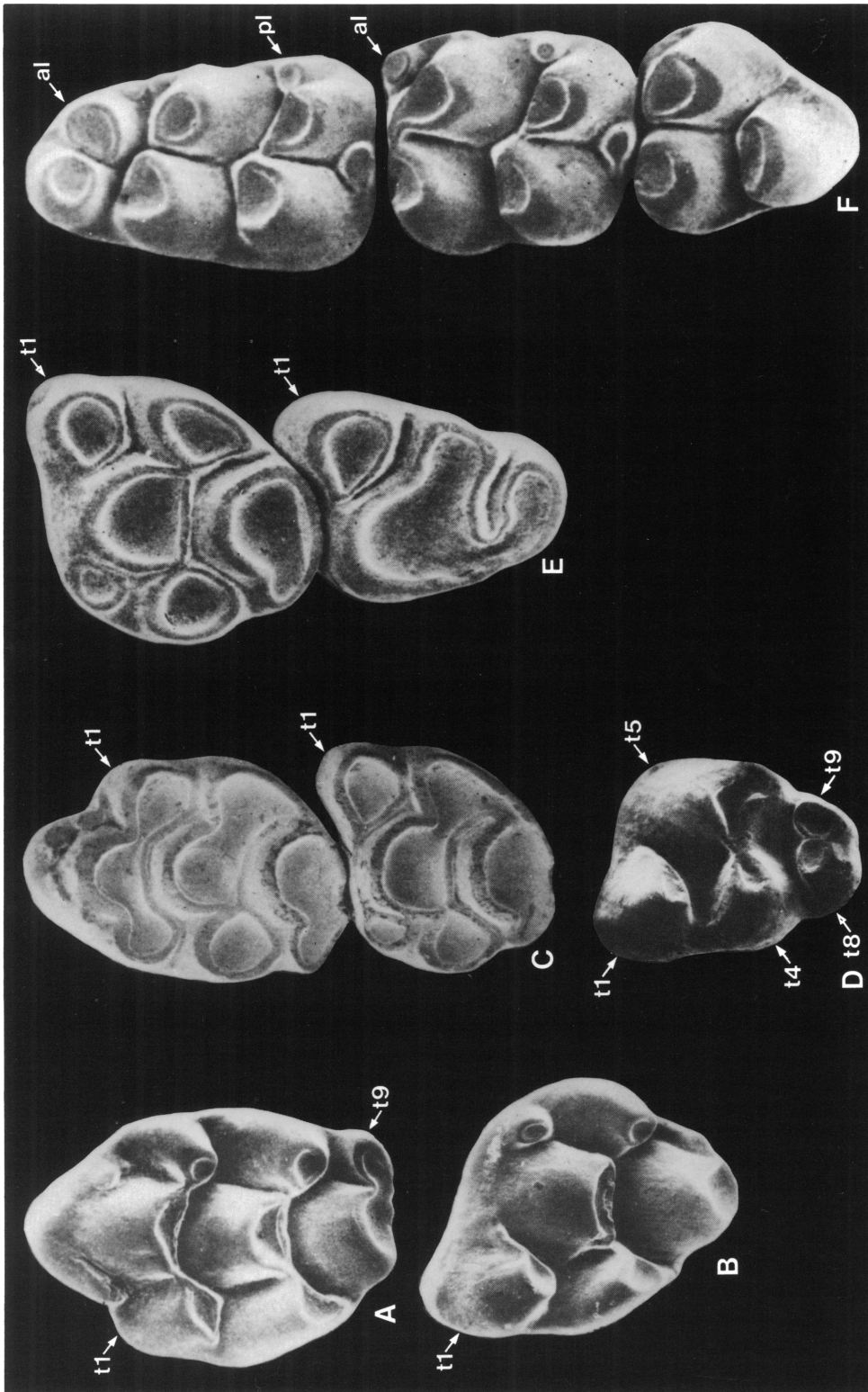


Fig. 11. Molars of *Golunda gurai* from the Pliocene Hadar Formation in northeastern Ethiopia. A and B, left first and second upper molars of young adults; C, first and second upper molars from old adults; D, left third upper molar from young adult; E, right second and third upper molars of adults; F, adult right lower molars. Abbreviations are explained in figure 10. See text and compare these views with those in figure 10. Reproduced from plate 2 in Sabatier (1982), where he provided measurements and identification numbers.



Fig. 12. Cranium of adult *Golunda ellioti* (AMNH 150077). Arrows point to traits discussed in text that contrast with the cranium of *Mylomys*; see figure 13. $\times 3$.

either a small round or ridgelike cusp in all the *Golunda* at hand. Shapes of the second and third upper molars in *Golunda* are derived compared with shapes of those teeth in *Mylomys*.

In the lower molars of *Mylomys*, shapes

and positions of the two cusps forming the anterior lamina of the first molar are more like those in *Pelomys* than *Golunda*, a primitive configuration. The rest of the occlusal surfaces, however, are more derived than those in *Golunda*: extreme reduction of cin-



Fig. 13. Cranium of adult *Mylomys dybowskii* (AMNH 241195). Compare features identified by arrows with those in figure 12. $\times 3$.

gular structures, anteromedial extensions of the crescentic cusps, loss or severe reduction

of the hypoconid on the third molar, and a labial root beneath the second molar.

When examined closely, specimens of *Mylomys* and *Golunda* also differ in cranial features (figs. 12, 13), as detailed below:

1. the zygomatic plate arises dorsally from its base to half way up the rostrum, the anterior margin is slightly concave, and the anterodorsal edge extends forward to nearly obscure part of the premaxillary-maxillary suture (in *Golunda*, the plate is taller, reaching three-fourths or more of the way up the side of the rostrum, its anterior margin is straight or nearly so and well posterior to the premaxillary-maxillary suture);
2. squamosal root of the zygomatic arch originates low on side of the braincase and below the suture outlining ventral margin of the parietal bone (each root originates higher on side of the braincase in *Golunda*, at the same level as ventral margin of the parietal, and that suture is hidden behind the horizontal ridge of the zygomatic root);
3. area of interparietal, seen in dorsal view, is usually absolutely small and always small relative to dorsal area of the braincase (the interparietal is usually absolutely larger, and always larger relative to braincase area in *Golunda*);
4. in the squamosal dorsal to the auditory bulla there is a large notch marking the squamoso-mastoid foramen (posterior margin of squamosal is complete in *Golunda*);
5. incisive foramina are long, their posterior margins extend beyond anterior alveolar margins of the upper molars (shorter in *Golunda*, ending well anterior to alveolar margins of first molars);
6. auditory bullae are smaller relative to size of braincase (relatively larger in *Golunda*).

Expressions of the cranial traits described here for *Mylomys* are also found in species of *Pelomys* and many occur in species of *Lemniscomys* as well. Cranial characteristics of *Mylomys* and *Pelomys* are much alike not only in general conformation of the skull but in structural details. Together they resemble *Golunda* in basic cranial shape but contrast with that genus in most of the characters discussed above.

A final comparison between *Mylomys* and *Golunda* reveals an important difference in

external features, even though both genera have a similar arvicanthine gestalt. Each front foot of *Mylomys* has three long fingers (digits 2–4). The first digit (hallux) is represented by only a round nail pressed against the side of the foot level with the posterior set of interdigital pads, a common configuration among muroid rodents. The fifth digit is a short mound covered with an attenuated claw situated opposite the first digit and extending anteriorly no farther than the base of the posterolateral interdigital pad. To all appearances the foot has but three functional digits; this morphology is usual in species of *Pelomys* and *Lemniscomys*. Structure of the first digit in *Golunda* is very much like that in *Mylomys*; the second, third, and fourth digits are also long; but the fifth digit extends anteriorly past the base of the fourth digit and bears a claw; the relative shapes and proportions of palmar surface and digits in *Golunda* are similar to that seen in *Hadromys* (see the figure in Roonwal, 1954) and *Arvicanthis*. Compared to *Golunda*, the front feet of *Mylomys* are more specialized and this derivation is shared with species of the African *Pelomys* and *Lemniscomys*.

My limited comparisons reported here lead me to disagree with the close phylogenetic relationship between *Golunda* and *Mylomys* that has been proposed by other observers. *Golunda* may be a member of an arvicanthine cluster of genera but many of its derived characters are not shared with *Mylomys*. The cranial and external traits that contrast *Golunda* and *Mylomys* bring together *Mylomys* and *Pelomys*. Both *Golunda* and *Mylomys* have large and crescentic isolated cusps (which represent a slight exaggeration of cusp shape and position in *Pelomys*) but other dental traits thought to ally *Golunda* and *Mylomys* are not as persuasive when molars are examined closely. The inclined orientation of cusp t1 on each molar; elongation of the second molar at its lingual and anterior margins, which gives cusps t3 and t6 a stretched appearance; third molar that is stretched along its anterolingual-posterolabial axis; and the large columnar cusps that form the posterolabially slanting anterior lamina on the first lower molar, along with an anteroventral cusp, are all specializations unique to *Golunda*. *Mylomys* has derivations of its own (small

cusps t3 and t9 on second molar, loss of cusp t9 on the third, loss of most labial cingular structures along lower molars, stretched anteromedial portions of crescentic cusps on lowers, reduction or loss of hypoconid on third lower molar, labial root on second lower molar) but except for these the basic cusp patterns are more like those seen in species of *Pelomys*.

Still, Asian *Golunda* shares some characters with living species of African arvicanthines and supports some zoogeographic link between Asian and Indian faunas. Judged by the kinds of morphological similarities and dissimilarities in the two clusters, there is basis for accepting a hypothesis of indirect affinities in the sense that *Golunda*, as known by morphologies of *G. ellioti* and *G. kelleri*, represents an independent derivation from an ancestral arvicanthine-like stock that once had Asian and northern African distributions. This seems a reasonable hypothesis based on samples of living and fossil Asian *Golunda* and living members of the arvicanthines, but how does it stack up against information derived from samples of Pliocene fossils from Ethiopia that have been identified as *Golunda*?

Golunda gurai was described by Sabatier (1982) from samples of cranial and dentary fragments as well as molars and incisors collected in the Pliocene Hadar Formation that outcrops in the Afar Depression of northeastern Ethiopia. The fossils came from strata originally deposited 3.1 to 2.9 million years BP. Samples of the same species were described in 1984 by Wesselman who studied isolated molars that had been obtained from sediments in the Shungara Formation in the lower Omo River valley of southwestern Ethiopia. The time span sampled was approximately 3 to 2.5 million years ago. Both Sabatier (1982) and Wesselman (1984) have described the dental differences between the Pliocene samples and those of Pleistocene *G. kelleri* and living *Golunda*, contrasts that are of far greater magnitude than those distinguishing *G. kelleri* from *G. ellioti*, but despite these differences, Wesselman (1984: 121) has concluded that "*Golunda gurai*, *G. kelleri*, and *G. ellioti* are very similar in their overall morphological pattern. The presence of other fossil taxa with Asiatic affinities . . . within

the sediments of the Omo Beds and within those of the Hadar Formation . . . supports the hypothesis that these different species of *Golunda* issue from a common ancestral stock rather than from two separate though convergent lineages." He agreed with Sabatier (1982) that the occurrence of *Golunda* in the Pliocene strata of Ethiopia supported the hypothesis of an African origin for the genus, an idea previously advanced by Jacobs (1978), but disputed by Brandy et al. (1980).

I have not examined specimens of the Pliocene *Golunda gurai* from Ethiopia; my knowledge of the species comes from Sabatier's (1982) original description and illustrations presented there and Wesselman's (1984) report on the specimens from the Shungara Formation in the Omo River valley. Sabatier's (1982, pl. 2) illustrations of selected specimens are good enough to permit the comparisons described below between dental characters of the Pliocene species and those of Asian *Golunda* (using *G. ellioti*); compare figures 10 and 11.

1. Enamel faces of the upper incisors are smooth in *G. gurai* but deeply grooved in *G. ellioti* (and the Pleistocene *G. kelleri*).

2. Cusps t1 and t4 on the lingual side and cusp t6 on the labial side of the first and second upper molars in *G. gurai* are not as elongated along either their anterolingual or anterolabial axis as they are in *G. ellioti*, and the occlusal surfaces are oriented posterior to the large central cusps rather than strongly slanted anterolabially and anterolingually (compare figs. 10 and 11).

3. Cusp t9 on the first molar in *G. gurai* is much larger relative to the central cusp t8 and juts out farther labially; it is almost as large as the two labial cusps anterior to it. Cusp t9 on the first molar of *G. ellioti* is relatively very small and usually directed anteriorly; it never forms a large posterior member of a labial cusp row.

4. The first molar of *G. gurai* is conspicuously longer than wide; in *G. ellioti* the molar is wider relative to its length and appears squat. The anterolingual cusp (t1) and margin of the second molar in *G. gurai* is enlarged along an anterolingual axis in slightly worn molars but not to the marked degree seen in *G. ellioti*; in worn second molars of *G. gurai*,

the configuration of the anterior occlusal outline is not too different from that of other arvicanthines.

5. The third upper molar of *G. gurai* is longer relative to the others in the toothrow compared to proportions in most species of arvicanthines (compare fig. 11 with fig. 8) and cusp t1 is relatively large and juts out to the lingual and anterior sides, features reminiscent of the third molar in *G. ellioti*; the proportions, however, are different. The entire third molar of the latter is elongate and appears stretched along an axis extending from the anterolingual to the posterolabial margin of the tooth. But it is the spectacular contrast in occlusal patterns that really separate the two species. The third molar of *G. ellioti*, as I described on previous pages, is highly modified; that tooth in *G. gurai* is not. Except for its length, the cusp pattern on the third molar of *G. gurai* is very similar to that characteristic of *Pelomys*: there is a large cusp t1, a medium-size cusp t4 united with a very large cusp t5 to form an arcuate lamina, and small columnar cusps t8 and t9 which coalesce with wear into an oblong (in occlusal view) lamina at the back of the tooth. *Golunda gurai* and *G. ellioti* share comparable cusps on each third molar but their shapes, relative sizes, and positions relative to one another are completely different (contrast figs. 10 and 11).

6. The first lower molar of *G. gurai* lacks an anterocentral cusp at the front of the tooth; such a cusp is present in *G. ellioti*. The anterolabial cusp of the front lamina is much larger relative to the anterolingual cusp than in *G. ellioti*.

7. In *G. gurai*, the anterolabial cusp of the second lower molar is appreciably larger relative to the protoconid and is situated more on the anterolabial margin of the tooth; the comparable cusp is small in *G. ellioti* and is located more to the lingual side; the protoconid is larger than that cusp in *G. gurai*. There is more of a cingular labial ridge on the second molar of *G. gurai* and a prominent posterior labial cusplet on that tooth. Only a remnant of a cingular labial ridge exists on the second molar of *G. ellioti* and it lacks a posterior labial cusplet.

8. The third lower molar of *G. gurai* has a cingular ridge on the anterolabial margin of the tooth that probably represents the base

of the anterolabial cusp. The hypoconid is absent, and the entoconid sits in the middle of the tooth and in occlusal view forms the rounded apex of the triangular third lower molar. On the third molar of *G. ellioti*, there is no cingular ridge or cusp, a small hypoconid is present, and the wide entoconid is situated on the lingual side so that it is aligned with the lingual cusps anterior to it in the toothrow.

9. The first lower molar of *G. gurai* lacks a lingual root; in addition to the other roots anchoring the first molar in *G. ellioti* (and the Pleistocene *G. kelleri*) there is a robust lingual root.

In my opinion, *Golunda* has not yet been found in the Pliocene outcrops of Ethiopia. Some of the dental characters used to diagnose *gurai* are reminiscent of the dental specializations seen in samples of Asian *Golunda* (mainly the inclined crescentic cusps on all molars and the enlarged cusp t1 on first, second, and third upper molars) but both *G. ellioti* and *G. kelleri* are characterized by dentitions that are far more highly derived than anything seen in samples of *gurai*, and most of these derivations are not shared with that Pliocene species. Most notable are the shape and occlusal pattern of the third molar. That tooth is long and robust in *gurai* but its cusp pattern is basically similar to those of other African arvicanthines and unlike the pattern in either *Golunda ellioti* or *G. kelleri*. The long and wide third molar does not necessarily indicate affinity with *Golunda*; similar proportions are characteristic of Pliocene *Saidomys* from Ethiopia (Sabatier, 1982) and living *Dasymys* (Misonne, 1969), for example. The highly derived cusp configuration of *Golunda* is unique to that genus.

The taxon *gurai* should be removed from *Golunda*. The specimens of that species from the Omo deposits were originally assigned to *Pelomys*, although only provisionally so (Jaeger and Wesselman, 1976) and perhaps that is where *gurai* should be placed until a better understanding of the variation in dental morphologies among both fossil and living species of arvicanthines is available.

Golunda, like *Hadromys*, appears to be indigenous to the Indian subcontinent. If it is really a member of the *Arvicanthis* Division, its ties to that African assemblage may be

hidden in the morphology of some late Miocene or early Pliocene ancestral population. Conceivably, Indian *Golunda* could have been derived from a stock resembling the Ethiopian *gurai* but in the face of the marked dental dissimilarities between *gurai* and *Golunda* and our ignorance of the fossil record of either *Golunda* or arvicanthines in general between Pliocene and lower Pleistocene times in Asia, the most reasonable hypothesis is that the dental traits of *gurai* represent moderate specializations developed from an arvicanthine ancestor, and that *gurai* became extinct without issue by about 2.5 million years ago (see also Denys and Jaeger, 1986: 223). And what about *Golunda*? In his treatise on Siwalik murids, Jacobs (1978) diagrammed his interpretation of the phylogenetic affinities among the Siwalik fossil species and indicated a derivation of *Golunda kelleri* from late Miocene *Parapelomys robertsi*—with a question mark. The evolutionary transformation of an ancestral population with morphology similar to *Parapelomys* may be the best hypothesis to explain the origin of Pleistocene *Golunda kelleri* and its very close relative, *G. ellioti*. A similar scheme (but deriving *G. kelleri* from Afghanistan *Parapelomys charkhensis*, also with a question mark, was suggested by Brandy et al. (1980). Sampling Siwalik strata deposited in the interval between late Miocene and early Pleistocene may reveal whether *Golunda* had its roots in Asian Miocene or evolved outside Asia and was a late immigrant to the Indian subcontinent.

Mus

A species of *Mus* is the third taxon identified in the fossils collected at the early Pleistocene site in the Pabbi Hills (Jacobs, 1978). The few isolated molars in the sample require careful comparisons with samples of living and fossil *Mus* from Asia and Africa. Those species endemic to Africa are regarded as comprising either a distinctive subgenus within *Mus* (Marshall, 1986) or a genus—*Nannomys*—not closely related to Asian *Mus* (Bonhomme, 1986). Both Wesselman (1984) and Sabatier (1982) have described fossil teeth of *Mus* which were found in Pliocene strata in Ethiopia. Wesselman's specimens are similar to the *Nannomys* group as represented by *Mus minutoides*. Sabatier (1982) would

align his specimens with the group that includes *M. musculus* and *M. booduga*. Specimens of fossil *Mus* from other regions in Africa have been identified as either distinctive species similar to those in the *M. booduga* group, as *M. minutoides*, or simply as *Mus* sp. (Wesselman, 1984). Asian fossil *Mus* are represented by *M. auctor* from the late Miocene of northern Pakistan (Jacobs, 1978) and *M. elegans* from early Pliocene strata in Afghanistan (Sen, 1983). Affinities of *M. auctor* are uncertain but dental morphology of *M. elegans* resembles that of *M. booduga*. Until the Siwalik Pleistocene specimens of *Mus* can be positively identified, their contribution to zoogeographical relationships, or lack of any, between the Indian region and northeastern Africa remains sketchy.

?*Millardia*

The two molars from Locality DP 24 in the Pabbi Hills that Jacobs (1978) regarded as indeterminate represent a fourth Pleistocene species (if both teeth are from the same taxon). To me, and my identification is tentative, the two teeth resemble those in samples of *Millardia* from the Indian region. Cusp pattern and number of roots on the first lower fossil molar closely resemble the patterns in *M. kathleenae* except that the posterior labial cusplet in the fossil is minute (large in *M. kathleenae*) and the tooth is much smaller. The fossil second upper molar also resembles cusp configurations in *M. kathleenae* except that the fossil is again smaller and cusp t9 appears absent because it has mostly coalesced with cusp t8 (cusps t9 is distinct in *M. kathleenae*). Neither of the two teeth from Locality DP 24 are like the molars from Hadar that Sabatier (1982) identified as *Millardia taiebi* and *M. coppensi*. Whether the fossils from the Pabbi Hills prove to be a Pleistocene species of either *Millardia* or a new genus, they apparently represent another native Indian element in the Pleistocene murine fauna of northern Pakistan.³

³ The recent record of *Rattus* from the Pinjor Formation of the Upper Siwaliks of India (Gaur, 1986) is based on a right upper molar that is not from *Rattus*. Judged by its size and morphology, the tooth resembles those of *Millardia*, especially *M. kathleenae*.

FINAL NOTES

Hadromys is distinctive. The combination of characters described earlier in this report provide partial definitions of morphological limits for the genus and for the living species, *H. humei*. Adding traits of the Pleistocene *H. loujacobsi*, which restricts us to first and second upper molars only, *Hadromys* can be diagnosed by: its coronal hypsodonty; simple cuspidation resulting in either arcuate or nearly straight laminae; no cusp t7 or posterior cingulum; a cusp t9 that is either ridge-like or columnar and juts anteriorly to coalesce with cusp t6 after some degree of wear; and first molars anchored by either four or five roots. Fossil fragments of *Hadromys*, especially molars, should be easily identifiable.

Not so easy to identify is the nature of faunal affinities between the Indian and northeastern African murine faunas. Geographic distributions of two species overlap the two regions. *Acomys cahirinus* ranges from southern Pakistan through southern Iran, southern Asia Minor, onto the islands of Cyprus and Crete, then through Saudi Arabia, Yemen, Jordan, Israel, and the Sinai Peninsula to northern and western Africa (Egypt, Libya, Mauritania, Morocco, Nigeria, and southern Algeria) and eastern Africa (Ethiopia, Somalia, Kenya, and Tanzania to Zimbabwe). *Nesokia indica* now ranges from Chinese Turkestan and southern Russian Turkestan through parts of Nepal, northern India, Bangladesh, Pakistan, Afghanistan, Iran, Iraq, Syria, Israel, northern Saudi Arabia, and into northern Egypt. Specimens from Paleolithic sites have been found elsewhere in Egypt and south to northern Sudan where the species now no longer lives (see the references in Osborn and Helmy, 1980: 314). Other than these two rats, no member of the modern murine fauna native to the Indian subcontinent (species of *Srilankamys*, *Cremnomys*, *Millardia*, *Golunda*, *Hadromys*, *Diomys*, and some species of *Mus* and *Rattus*) has been found in northeastern Africa, and no species native to northeastern Africa now occurs also in the Indian region. *Arvicanthis niloticus* is recorded as a member of the modern fauna in southwestern Arabia (Harrison, 1972) and the genus is known from late Pleistocene fossils in Israel (Tchernov, 1968). *Pra-*

omys fumatus, which ranges through northeastern Africa, also occurs in Yemen and southwestern Saudi Arabia (Nader et al., 1983), and the related genus *Mastomys* is represented by late Pleistocene fossils in Israel (Tchernov, 1968). Aside from these three, no other species of indigenous African murine gets any closer to the Indian subcontinent. The only other typically African genus that is thought to occur outside of the continent is *Pelomys*; the determination is based on fossil molars collected in late Pliocene strata on the island of Rhodes but the identity is provisional and the sample may represent some genus other than *Pelomys* (Bruijn et al., 1970).

Identifications of Pliocene murine samples from Egypt, Ethiopia, and Afghanistan have been used as evidence for faunal exchange between northeastern Africa and Asia. The genus *Saidomys*, first documented by samples collected in Wadi el Natrun, northwest of Cairo, Egypt (Slaughter and James, 1979) has been recognized in Pliocene sediments of Afghanistan as *S. afghanensis* (Sen, 1983), in the Pliocene Hadar Formation of Ethiopia as *S. afarensis* (Sabatier, 1982), and in the Pliocene Shungura Formation of the Omo River valley in Ethiopia as *Saidomys* sp. (Wesselman, 1984). The presence of *Saidomys* in Egypt and Ethiopia, as well as *Golunda* in the Pliocene of Ethiopia prompted Brandy et al. (1980) to recognize a new faunal province at the boundary between Miocene and Pliocene zones. Sabatier's (1982) subsequent addition of two species of *Millardia* and a species of *Mus* possibly allied to the Asian *M. booduga* group reinforce a past biogeographic affinity between central Asia and northeastern Africa during Pliocene times, at least in the Hadar region. And, wrote Wesselman (1984: 199), the "Asiatic forms at Hadar are dominant in terms of numbers of specimens and Jaeger (pers. comm.) feels that Hadar may have been connected with Asia to the east, that it was probably at higher altitude than it is today, and that it was probably separated from the Omo Valley by the Ethiopian highlands and possibly by relict Central African forests and arid zones as well."

The Pliocene Hadar rodent assemblage is so different from other East African fossil faunas that Denys (1985) has suggested that it

defined a distinctive biogeographic subprovince; the presence of samples identified as *Saidomys*, *Golunda*, and *Millardia* certainly influenced her analysis. Removing *Golunda* from the assemblage, as I explained should be done, decreases the strength of the Asian connection but not the endemism of the Hadar region. The taxon *gurai*, and the species identified as *Saidomys* and *Millardia* have not been found elsewhere in Africa outside Ethiopia except in Egypt (*Saidomys*).⁴

Before an Asian–northeastern African connection during Pliocene is accepted as past reality, examples of the *Saidomys*, *Millardia*, and *Mus* should be carefully restudied. Morphologies of specimens in the *Saidomys* samples should be compared with those in both fossil examples and Recent specimens of genera in the *Arvicanthis* Division. Possibly except for *Lemniscomys*, the morphological limits of species and genera in that cluster are obscure; the group requires careful taxonomic revision. *Saidomys* is considered to be an arvicanthine (Slaughter and James, 1979) and future inquiries should determine whether the Egyptian and Ethiopian *Saidomys* tie closer to African arvicanthines than to Afghanistan *Saidomys* or if all the geographic samples of *Saidomys* are really closely related; nothing less than a careful revision of what is now identified as *Saidomys* is needed, set in the framework of comparing the fossils with *Karimata* and *Parapelomys* on the one hand and samples of living arvicanthines on the other.

The Indian *Millardia* and closely related *Cremnomys* consist of species that also require taxonomic revision to determine ranges of individual and species variations in morphologies. There is not even a good definition or diagnosis of either genus. Any revisionary study should reexamine the fossils from Hadar to determine if they are really examples of *Millardia* and to test the hypothesis that what is now an Indian group actually occurred at a past time in what is now northeastern Africa.

⁴ This statement reflects current sampling distribution but whether or not it estimates actual past geographic distributions in Africa can be determined only after other regions are worked; the Pliocene and Pleistocene of much of Africa has yet to be sampled for murines.

It is an exciting time for students of murid phylogenetics and biogeography. Excellent collections of fossils and studies based on them are supplementing inquiries into species definitions and geographic distributions of living species. Glirologists, whether neontologists or paleontologists, can now turn to both fossil and Recent samples to answer questions about evolutionary histories of species groups and faunas. Although much new information is available, more work needs to be done, especially defining species limits and formulating hypotheses of phylogenetic and biogeographic relationships of murines native to the Indian subcontinent and those originating in Africa.

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